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THE UPPER MIOCENE AESHNIDS OF MONTE CASTELLARO, CENTRAL ITALY, AND THEIR RELATIONSHIPS TO EXTANT SPECIES (ANISOPTERA: AESHNIDAE)

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30 wings and 3 abdominal segments from the Lower Messinian "Strato degli insetti" nr Pesaro are described, analysed and compared with the extant taxa. *Anax cryptus* sp.n., *Aeshna ghiandonii* sp.n., *A. messiniana* sp.n. and *A. multicellulata* sp.n. are described and illustrated. 5 out of 10 more or less entire *Anax* wings are indistinguishable from *Anax imperator*, but the majority of the *Anax* and *Aeshna* fragments could not be assigned to a definite sp. – The monophyletic nature of the *Anax* group is emphasised, and the genus-group name *Hemianax* Selys, 1883 suppressed.

INTRODUCTION

The present paper deals with the review of the 6 million years old Upper Miocene (Lower Messinian) adult dragonflies from the Monte Castellaro deposit, referable to the Aeshnidae, and recovered during 1974-1991. The dragonflies are preserved as compression fossils in a well-cemented marly layer called "Strato degli insetti" (GENTILINI, 1986), outcropping in the higher part of the facies "Marne bituminose". In this special level larval stages of dragonflies are absent. The absence of larvae, which are very abundant in the underlying strata, might be due to the conditions of the sedimentary basin, characterized by a variable salinity, with an ichthyofauna dominated by *Aphanius crassicaudus* possessing traces of pachyostosis.

Dragonfly remains occur with numerous insects, leaves, fishes and rare spiders, molluscs and birds, representing a temperate to warm-temperate habitat. The first record of insect remains at Monte Castellaro was published by GENTILINI

(1975); descriptions of new arthropod species followed (GENTILINI, 1986; 1989). The geology of the Messinian of the Pesaro area was studied by SAVELLI & WEZEL (1979) and the fish faunas by SORBINI & TIRAPELLE RANCAN (1980) and by SORBINI (1988).

Fossil insects have been recovered from two sites of the Monte Castellaro section, along the Adriatic Sea in the vicinity of Pesaro town (Marches, Central Italy). The outcrop is included in the "Gessoso-solfifera" formation, Lower Messinian, and contains four facies composed of clayey marls, diatomite, bituminous marls and sandstones. Insect remains occur exclusively in fine-grained bituminous marls, deposited in a coastal lagoonal environment surrounded by wood-clad hills. The climate was probably warm-temperate but with a tendency to deterioration toward a moderately cooling phase, as suggested by insect and plant remains.

Of the thirteen insect orders represented in the Messinian sediments of Monte Castellaro, only four families of Diptera (Limoniidae, Trichoceridae, Tipulidae and Bibionidae) and two of Odonata (Libellulidae, Corduliidae) have been so far studied (GENTILINI, 1986, 1989, 1990). Numerous fossil insects still remain unidentified at the family, subfamily and genus level. Only a list of orders, with number of specimens and percentages has been previously recorded. On the other hand the odonates are comparatively well known. Six families are represented in the deposit: three in each of the suborders Anisoptera and Zygoptera. The most common species belong to the Libellulidae and Aeshnidae with more than 80% of specimens, while the Corduliidae and Zygoptera are very infrequent.

Future findings may add more specimens to the material substantiated in this review. Male hindwings and basal abdominal segments of males are urgently needed to confirm the number of aeshnid species in the "Strato degli insetti" as well as to allow taxonomical considerations using the argumentation of phylogenetic systematics.

METHODICAL REMARKS

From all specimens presented in this paper, careful drawings have been prepared in order to calculate dimensional proportions in wing venation, abdominal segments and appendices, important for diagnostical conclusions. All absolute measurements were taken directly from the fossils. The measured distances at the wing surface have been illustrated by PETERS (1991, p. 164, fig. 1). The main wing veins are named in accordance with the evolutionary founded nomenclature of RIEK & KUKALOVA-PECK (1984). Its comparison with the Tillyard/Fraser system and a list of abbreviations, customary in the terminology of Odonata wing venation, is presented in the paper on the Monte Castellaro libellulids (GENTILINI, 1989, p. 255).

ANAX LEACH, 1815

Material. – 12 forewings (Nos 154, 155, 156 l, 156 r, 157A, 158A, 159A, 160 l, 160 r, 1209A, 1210, 1218; 9 hindwings (Nos 185, 193, 197A, 198, 1211, 1215, 1216, 1217/1217A, 1219; 3 wing tips (Nos 147/147A, 182, 195); 2 fragments of ♂ abdomen (Nos 210, 211/211A). Locality: Monte Castellaro, Marches, Central Italy. Age: Upper Miocene (Lower Messinian); level "Strato degli insetti", facies "Marne bituminose"; formation "Gessoso-solfifera".

Some wings are nearly totally preserved (Figs 1-3, 14), the majority only partly. For the wing tips a decision whether they are parts of fore- or hindwings was impossible. Several wings and wing fragments due to plastic deformation during fossilisation and/or tectonical burden and stress afterwards (synsedimentary and syndiagenetic processes, C. Brauckmann, in litt.) are stretched or shortened and in the latter case may show an undulated hind margin (Fig. 6).

The material of *Anax* specimens as well as the specimens referred to the genus *Aeshna* (see below) are stored in the Monte Castellaro working collection of the first author.

DIAGNOSIS (NEW SYNTHESIS). — All above listed specimens of fossil wings in total or to a different extent (if fragmented) bear the complex of venational characters qualifying the *Anax* group within the Aeshnidae: (1) anterior part of Arc shorter than its posterior segment, (2) RP diverging near the midst of the anterior part of Arc, (3) MA-fork and the conjunction of its anterior branch with RP_{3-4} very distinct, (4) Mspl and Rspl deeply arched, (5) between IR_2 and Rspl some distinct slanting rows of rarely less than 5 cells, (6) IR_2 unforked (its pseudofork starting beneath Pt embraces only 2 rows of cells), (7) RP_1 distinctly curved towards Pt (Fig. 4a), (8) A_2 in hindwing running parallel to A_3. The male abdominal appendices of No. 211 (Fig. 12) are constructed as typical for *Anax*.

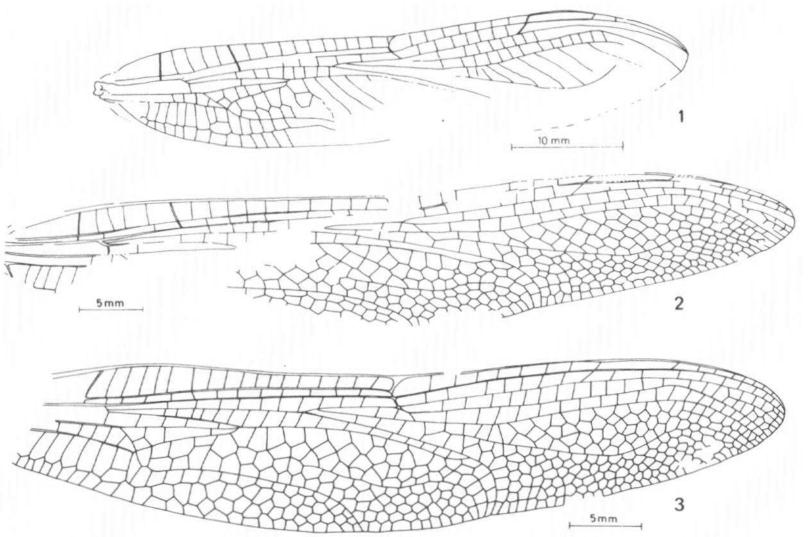
On the other hand the fossils possess no combination of characters by which other Aeshnid groups (genera) are distinguished from *Anax*. The members of the *Anaciaeschna* group (excluding *Aeshna isosceles*) have the majority of the characters mentioned in common with *Anax*, aside of their peculiarities in the wing base and the second male abdominal segment, and in the configuration of head, they are quite different from *Anax* by the presence of a true IR_2-fork which embraces 3-4 rows of cells (Fig. 4).

It should be mentioned that in case of fossil material, *Anax* males, due to the female-like construction of their hindwing bases and second abdominal segment, can be detected only by the contour of appendices and (if preserved) by the presence of the fossa genitalis.

Five of the more or less complete *Anax* wings preserved distinct colour markings (GENTILINI, 1989), viz. forewing 157A, hindwings 185, 1209A and 1210 are tinted grey yellowish or pale yellow, and hindwing 198 is pale brown. Other wings, for example forewings Nos 158A, 159A and 160 as well as hindwing No. 1219 are hyaline in appearance. Colour traces in the wing membrane cannot be interpreted as indicative of females. Freshly emerged *Anax* specimens of both sexes bear fumose wings, and there are mature males with pale yellow or also greyish yellow tinted wings.

COMPARISON. — At first glance, the fossil *Anax* wings and their fragments seemed indistinguishable from wings of the extant *A. imperator*. But the small dimensions of the only slightly deformed hindwing No. 1219, the last discovered specimen of our series of Monte Castellaro *Anax* fossils, caused us to pay close attention to the length differences and to carefully calculate the results of deformation of the wings by comparison with the natural configuration of the wing membrane in extant species.

The relative breadth (maximal wing width in % of its length) has proved to be a useful index for estimating the degree of deformation in fossil wings. In *A. imperator*, *ephippiger*, *julius* and *parthenope*, taken as representatives of the group, the relative breadth of the forewing varies between 22.3 and 24.3%. Out of the five fossil *Anax* forewings, only No. 160 (Fig. 5), with an index of about



Figs 1-3. Forewings of *Anax* cf. *imperator*: (1) specimen No. 155; – (2) specimen No. 156 r; – (3) specimen no. 157A.

23%, fits the proportions of relative breadth in living *Anax* species. Three other specimens (Nos 155, 156 and 157A), by index values lower than 20%, express clear signs of being narrowed along the wing axis. The forewing No. 1209A (Fig. 6), by its cell configuration and the undulation of the hind margin, revealing its broadening in anterior-posterior direction, shows a corresponding high index of 31.4% (Tab. I).

Plastic deformation during fossilisation and/or syndiagenetic processes causing stretching of a wing, do not necessarily affect the whole membrane evenly. Due to its weaker consistence, the apical half of wing will be less resistant against stretching (lengthening) than its basal half; the same holds true for the frontal side of a wing in contrast with its posterior part. In order to test this conjecture, another index was introduced: the ''post/antenodal index''. This ratio expresses the distance between N and the proximal end of Pt in % of the distance between the first antenodal crossvein and N (measured along the wing border). In the forewings of extant *Anax* species, the ''p/a-index'', being species-specific and sex-dependent, varies from 62 to 82%. But in general, there is a steep positive linear relation between the absolute N-Pt distance and its relative length (p/a--index). The range of the indicated ratio variation is occupied by specimens with N-Pt distances from 11.0-15.0 mm in length. The fossil forewing No. 160 is in line with these conditions (12.1 mm; 63.4%). No. 157A (Fig. 3), in view of its

Table I

Diagnostically valuable measurements (in mm) and distance proportions (in %) of fossil *Anax* wings from Monte Castellaro in comparison with equivalent data of some extant *Anax* species (mean values or ranges of variation)

Coll. No. of fossil or species name	Length of wing	Relative breadth of wing	p/a ratio	Distance N-Pt in % of wing length	Pt length in % of distance N-Pt	Pt length in % of wing length	Length of T in % of wing length	Relative breadth of T
FOREWING								
155	51.4	19.6	61-65	24.4	46.4	11.3	14.4	23.9
156r	62.0	18.5	67	26.0	39.8	10.3	14.8	15.6
157A	52.9	19.8	67	26.1	39.9	10.4	15.1	20.7
160	47.0	23.1	63.4	25.7	40.9	10.5	15.1	26.4
1209A	42.1	31.4	63	25.0	41.2	10.3	15.9	31.7
imperator Leach	48.5-52.5	22.3-23.2	66-76	24.9-28.5 (26.8)	33.6-44.8 (33.8)	9.0-11.6 (10.5)	13.3-14.4	25.4-29.1
parthenope (Sel.)	44.1-51.2	23.2-24.3	76-82	26.5-29.3 (28.1)	29.0-36.6 (32.4)	8.0-10.2 (9.1)	13.7-15.1	23.9-29.4
julius Br.	49.9-53.6	23.5-23.9	66-70	24.6-27.2 (25.6)	35.7-44.8 (40.7)	–	–	–
ephippiger (Burm.)	43.5-49.5	22.4-23.6	62-69	24.0-27.4 (25.8)	37.4-55.4 (45.2)	9.8-13.3 (11.5)	15.7-17.3	19.8-22.5
papuensis (Burm.)	48.4-53.1	–	62-67	25.4-28.1	34.9-44.3	9.8-11.6 (10.8)	15.3	22.8-23.5
HINDWING								
185	49.2	34.3	96.1	31.1	35.8	11.1	11.8	40.4
197A	51.3	23-25	106.7	34.1	29.2	10.0-10.1	11.3-11.6	32.4
198	51.8-53.7	27.0	102.0	34.4-35.7	33.0	11.4-11.8	12.7-13.1	26.4
1215	42.4-42.9	40.0	99.1	33.7-34.1 (32.8)	31.8	10.7-10.8	12.9-14.0	38.6
1219	41.4	35.7	98.9	32.8	35.3	11.4	12.4	41.9
imperator	47.1-50.6	29.1-33.1 (31.0)	98-112	31.2-34.4 (33.0)	28.4-39.7 (34.0)	9.5-12.8 (11.4)	11.4-11.7	35.1-39.4
parthenope	44.1-50.4	29.3-33.1 (31.3)	102-115	31.9-35.5 (33.7)	26.2-32.7 (29.4)	8.6-10.6 (9.7)	11.7-12.6	33.3-38.6
julius	49.2-52.9	29.8-33.0 (31.3)	94-105	29.7-31.6 (30.6)	34.1-41.9 (37.4)	–	11.1-12.8	–
ephippiger	42.7-48.7	30.3-32.5 (31.8)	101-112	32.7-35.6 (34.1)	29.8-42.2 (36.0)	10.5-13.9 (12.0)	13.2-14.4	26.6-30.8
papuensis	47.0-51.8	29.0-30.8 (30.0)	97-105	32.1-35.4	28.9-35.8	10.2-11.9 (11.3)	12.6	35.5-36.0

greater N-Pt distance (13.8 mm), should bear a higher ratio than it does (no less than 70%), thus indicating heavier stretching of the basal half of the wing membrane. No. 156 (Fig. 2) possesses a very large N-Pt distance of about 16.1 mm (never seen in living species); its inadequately low p/a ratio of about 66.7%, based on our N-Pt distance of ''normal'' length (12.6 mm), again points to lengthening, (probably) of the basal half of the wing (the relatively long Pt may serve as additional reference). No. 1209A shows both a short N-Pt distance (10.5 mm) and a low p/a ratio (63.0%): thus the demonstrated broadening of the membrane is accompanied by some shortening of its apical half (Tab. I).

In summary, the measurable fossil forewings express the following kinds of deformation: No. 155 (Fig. 1) – stretching of the basal half; No. 156 – extreme stretching along the whole wing axis; No. 157A – lengthening mainly of the basal part of the membrane; No. 160 – nearly normal configuration; No. 1209A – broadening and some shortening of the apical part.

Of the hindwing remnants three specimens allowed making measurements: Nos 185, 198 (Figs 7, 9) and 1219 (Figs 11, 14). Two others (Nos 197A and 1215) allowed to determine with certainty only their p/a indices. In the above mentioned four *Anax* species, the relative breadth of the hindwing varies from 29.0 to 33.1%, almost the whole range of variation being met within *A. imperator* alone (Tab. I). The mean values are 31.0 (*imperator*), 31.8 (*ephippiger*) and 31.3 (*julius, parthenope*). In females the hindwing usually grows somewhat broader than in males, but with extensive overlap of variation. None of the calculated ratios of the relative breadth of the three fossil hindwings falls within the limits of variation of extant *Anax*. No. 185 (Fig. 7), having a nearly normal configuration, with an index of 34.3% comes nearest to the *Anax* condition. The index value of 35.7% for hindwing No. 1219 (Fig. 11) indicates a very broad wing membrane. In contrast with the calculated values its basal wing cells are not distinctly elongated backwards. Equal conditions seem to prevail in the partly preserved hindwing No. 1215 (Fig. 10) with an even higher relative breadth (about 40%). On the other hand, indications of cell deformation in coaxial direction are clearly seen in No. 198, accompanied by disruption of the wing tip (Fig. 9); its index of relative breadth is correspondingly low (about 27%).

With 96.1%, the value of its p/a index, hindwing No. 185 falls within the range of variation in extant *Anax* specimens, with absolute N-Pt length 15-16 mm. Thus, a nearly normal configuration of the wing seems to be confirmed. Hindwing No. 198, by its index value of 102%, documents an extremely stretched condition, completed by extraordinary length (52.0-53.7 mm) and a very long N-Pt distance (18.5 mm). The wings Nos 1219 and 1215 (the tip of the latter beyond Pt is missing), in contrast with the high values of relative breadth (35.7 in No. 1219), bear higher p/a ratios than the "nearly normal" No. 185 (98.9 and 99.1%). Even if some broadening of these wings cannot be excluded, there are no indications of their being shortened during or after fossilisation. And more than that: if the relatively high p/a index of both wings in face of their very broad wing membrane cannot be interpreted as an indication of stretching, the index values remain to be seen as a qualifying character state, supplemented by the small length of No. 1219 (41.4 mm only)!

Keeping in mind the ascertained data on the possible ranges of deformation in the fossil *Anax* wings, some comparisons can be made using their dimensions. There are only two extant *Anax* species bearing wings shorter than 48 mm (forewing) and 46 mm (hindwing): *A. parthenope* (only in central Europe, while it is larger in almost all other ranges of its distribution) and *A. ephippiger*. The fossil forewings Nos 160 and 1209 and the hindwing No. 1219 are with certainty not longer than 47 mm (47.0, 42.1 and 41.4 mm resp.). Specimen No. 1215 may

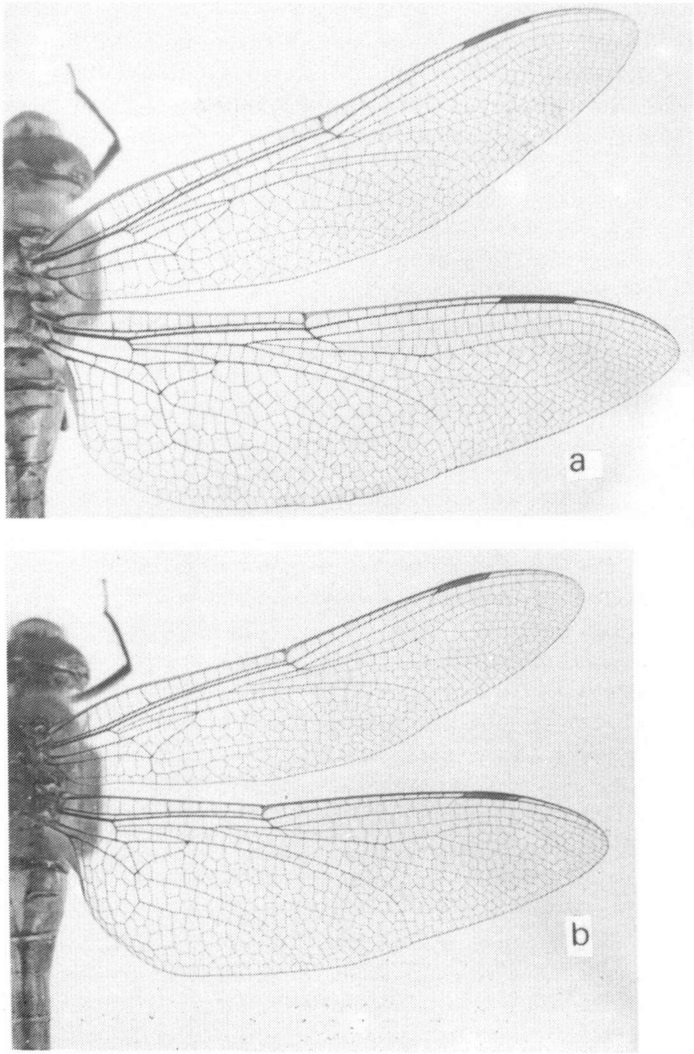
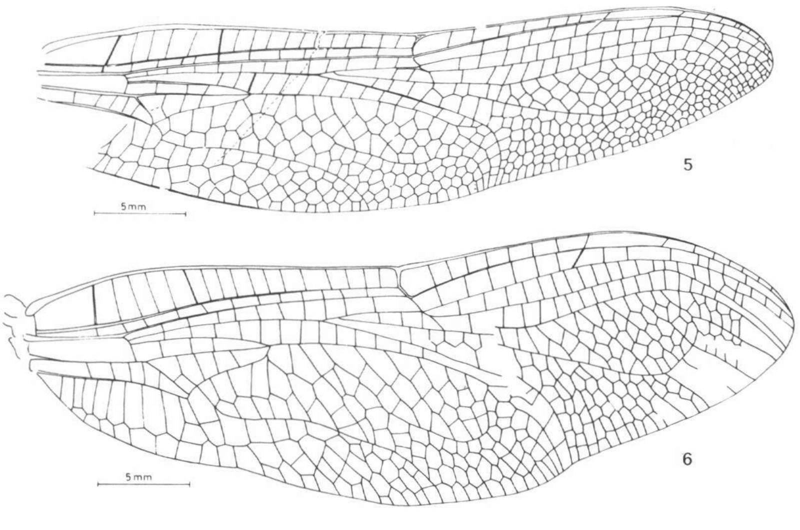


Fig. 4. Female fore- and hindwings of (a) *Anax imperator* Leach; — (b) *Aeshna isosceles* (Müller).

well be added to the three fossils mentioned: calculated from its N-Pt distance, the wing would have been no longer than 45.3 mm (most probably 42.4-42.9 mm; Tab. I) (the presumed strong linear dependence between N-Pt distance and wing length has been tested previously in the case of *A. imperator*, *parthenope*, *ephippiger*, *julius* and *junius*). Therefore there is no reason to speculate on possible affinities of these specimens with *A. imperator* or any other *Anax* species, whose wings usually measure more than 48 mm. It should be added that specimens with wings shorter than 48 or 46 mm are found in North American populations of *A. junius*. But this species possesses very long Pt (5.4 and more mm in forewing, 5.8 and more mm in hindwing), not seen in the short-winged *Anax* fossils.

The remaining measurable fossil *Anax* wings (forewings Nos 155, 156 and 157A, hindwings Nos 185, 197A and 198), with the exception of the extremely stretched forewing No. 156, fall within the range of length dimensions of large--winged *Anax*, such as *A. imperator, julius* or *speratus*. Bearing in mind the very small relative breadth of the wing No. 156 (18.5%) it should have been distinctly shorter "in life" than the 62 mm measured in the fossil.



Figs 5-6. *Anax cryptus* sp.n., forewings of the paratypes: (5) specimen No. 160; — (6) specimen No. 1209A.

After having introduced dimensions and some wing proportions into analysis and having compared the fossil *Anax* wings with those of extant species, as a preliminary result of our investigation it should be stated that the Monte Castellaro set contains at least two different species, a small-winged and a larger one. For the former the question of closer affinity to one or the other of living species has already pointed to either *A. ephippiger* or *A. parthenope*. Concerning the long-winged specimens, no indication could so far be presented and the question arises whether these represent only two or perhaps more species.

Intending to solve the affinity problem, the fossil *Anax* wings and samples of specimens of several extant *Anax* species (*imperator, parthenope, julius, ephippi-*

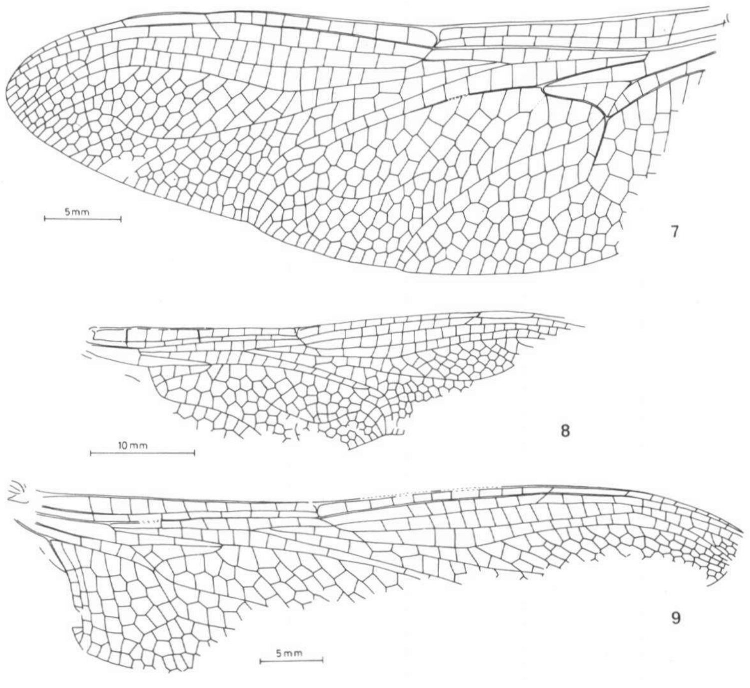
ger, *papuensis*, *speratus*, *junius*, *nigrofasciatus*, *guttatus*, *immaculifrons*) were analysed and compared with each other by registration and weighting of quantitative and qualitative characters in fore- and hindwing. Beyond the ones already introduced, the following characters have been checked: breadth of discoidal triangle, T (in % of its length), length of T (in % of wing length and in % of length of supratriangle, ST), height of bulge of RP_1 below Pt (expressed by the minimal distance between RP_1 and RP_2 in % of the maximal distance between RP_1 and IR_2), length (posterior extension) of the "anal triangle" compared with the length of anal loop, numbers of antenodal (Ans) and postnodal crossveins (Pns), of crossveins between primary Ans, in the supratriangle and anterior to the bridge vein between RP and IR_2, numbers of cells along the $RP_{3\text{-}4}$ proximal and distal MA-bifurcation, in T, in the longest oblique row between IR_2 and Rspl as well as between MA and Mspl, in the anal loop, paranal loop, "anal triangle", and the number of paired cells (including tripled ones) between MP and CuA (the four last listed countings only in hindwings).

In the small-winged *Anax* fossils the relative length of Pt has proved of diagnostic value: there are no specimens of *A. parthenope* possessing a Pt longer than 37% of the N-Pt distance in the forewing and 33% in the hindwing. In *A. ephippiger* the same ratio reaches from 37 to 55% and from 30 to 42%, respectively. Thus there is only a small overlap in the hindwing index values between the two species. The small fossil *Anax* forewings No. 160 (Pt/N-Pt index 40.9%) and No. 1209A (41.2%) fall within the variation range of relative Pt length characterizing *A. ephippiger*. Hindwing No. 1215, by its index value of 31.8%, is situated in the zone of *parthenope-ephippiger* overlap (Tab. I). This transgression can be minimized by calculating the index Pt length in % of hindwing length. The variation of this ratio reaches from 8.6-10.6% in *A. parthenope*, and from 10.5-12.4% in *A. ephippiger* (both indices of relative Pt length are not sex--dependent). In the hindwing No. 1219 the Pt length measures 11.4% of wing length; the calculations on the partly preserved short hindwing No. 1215 produced values between 10.7-11.1%, thus equaling the *ephippiger* ratio variation.

Another key condition is given by the already debated p/a ratio (its species--specific variation is not correlated with wing length). In the forewings of *A. ephippiger* the index varies from 62 to 69%; in forewings of *A. parthenope* the range extends from 76 to 82%. The small forewings Nos 160 and 1209A possess ratios of 63.4 and 63.0%! As to the hindwing p/a ratios, a broad overlap between the two species is present, but the lower values are found in *A. ephippiger* (101--112%; 102-115% in *parthenope*). The two small hindwings, with ratios of about 99 and 100%, are nearer to *ephippiger* than to *parthenope*.

In short: according to their small dimensions the fossil *Anax* wings Nos 160, 1209A, 1215 and 1219 cannot be compared with other extant species than *A. parthenope* and *ephippiger* (small North American *A. julius* are excluded by relatively very long Pt). Using the relatively clear-cut differences in Pt length indices and forewing p/a ratios between *A. parthenope* and *ephippiger* as a dividing criterion, we have to state that the individual ratios of the four small fossil wings fall well within the ranges of variation known from *A. ephippiger* (Tab. I). Thus in these features these fossils possess more affinities to the latter than to any other extant *Anax* species.

Looking for confirmation of the *ephippiger* affinity of the small fossil wings, only one additional indication was detected: there is a statistically proved difference between *parthenope* and *ephippiger* in the ratio N-Pt distance to length of forewing (mean values in *parthenope* 28.1+0.17%, in *ephippiger* 25.6+0.22%). The individual ratios of both small forewings (Nos 160 and 1209A), namely 25.7 and 25.0%, fall near the mean value of *ephippiger* and far outside the variation range of that index in *parthenope* (26.5-30.9%).



Figs 7-9. Hindwings: (7) *Anax* cf. *imperator*, specimen No. 185; – (8) *A.* cf. *parthenope*, specimen No. 197A; – (9) *A.* cf. *imperator*, specimen No. 198.

Bearing in mind some remarkable venational differences between *A. parthenope* and *ephippiger* (relative length of T, CuA branching, number of paired or tripled cells between CuA and MP) we have to note that the small-winged fossil *Anax* do not meet the diagnostical peculiarities of *A. ephippiger*. As will be pointed out later in this paper, the smaller *Anax* from Monte Castellaro, compared in this respect with *A. ephippiger*, persisted in a more plesiomorphic state.

Our attempts to determine the affinities of the nearly completely preserved larger *Anax* wings Nos 155, 156, 157A (Figs 1-3), 185 (Fig. 7), 197A and 198 (Figs 8, 9) developed into a very laborious task. We do not feel fully satisfied with the results, partly reached by hypothetical conclusions.

As to the first step of comparison, the relative length of Pt (Pt length in percent of N-Pt distance along the wing border) again has proved to be useful: in both fore- and hindwing the relative Pt length in *A. immaculifrons, speratus, nigrofasciatus, guttatus* (selected as representatives of the *guttatus* species group) and, as already shown, in *parthenope* is lower than the corresponding ratios in 5 of the 6 large fossil *Anax* wings (Fig. 13); the exception is No. 197A, with a Pt length ratio of only 29.2%.

A. junius may be left out, since its very high ratios of relative Pt length (particularly if calculated in % of wing length) do not fall within the data set of the fossils. The Pt ratio of hindwing No. 197A lies near the mean value for *A. parthenope* (29.2%). Looking at the variation ranges of *A. imperator* (28-40%) or *papuensis* (29-36%), the ratio of the fossil wing (29.2%) would be found near their lower limits. In *A. julius* the range of this character starts and ends with higher values (34-42%; Tab. I).

Hindwing No. 197A is stretched along the whole wing axis as indicated by its low ratio of relative breadth (23%, max. 25%). Nevertheless, the absolute measurements of the distances Ans-N and N-Pt (16.4 and 17.5 mm, resp.), being sharply different from the much extended measurements of the extremely stretched hindwing No. 198 (18.3 and 18.8 mm), are situated well within the known variation range in extant *Anax* species, viz. the measurements of both distances in almost all *parthenope* females and in single *imperator* and *papuensis* females (15-17 and 17-18 mm, resp.). Therefore their p/a ratios (105-115%) agree with the corresponding values in the fossil (106.7%). The latter bears 15 cells along RP_{3-4} (from the arculus down to the MA-bifurcation); their number equals the mean value in *A. parthenope* (14.9±0.14) and is rarely met within *A. imperator* (12% of specimens) and even less so in *A. papuensis* (9%).

On account of the low value of its relative Pt length, No. 197A needs to be compared also with *A. guttatus* and *nigrofasciatus* (in *A. immaculifrons* and *speratus* the Pt length ratios are even lower; Fig. 13). The fossil wing differs from the hindwings of the two species by the low number of cells (15) along RP_{3-4} (16-20 in *guttatus* and *nigrofasciatus*) and by the reduced number of Ans (10 against 11-13). *A. guttatus* usually bears 3-4 crossveins in front of the bridge vein, *A. nigrofasciatus*, *A. parthenope* and the fossil wing possess only two. Whereas the hindwing length of *A. nigrofasciatus* varies from 47 to 50 mm, No. 197A was not shorter than 50.5 mm. Combining all arguments on the qualities of hindwing No. 197A, it must be stated that the specimen most likely possesses closer affinity to *A. parthenope* than to any other of the above mentioned extant species.

After having used the "dividing power" of the relative Pt length in order to describe the affinities of the larger-winged *Anax* fossils (with the exception of No. 197A) only *A. imperator*, *julius* and *papuensis* remain for further comparison. In view of its recent range, *A. imperator*, widely inhabiting the Mediterranean area, should be the first candidate to be connected with the five larger Monte Castellaro *Anax* wings.

In the forewing the distance between N and Pt, expressed in % of wing length, may be used to separate most *imperator* specimens from those of *julius* and *papuensis*: the relatively few *imperator* with wings longer than 50 mm possess a higher N-Pt distance ratio (27.5-28.5%) than *julius* and *papuensis* specimens of equal forewing length (24.5-27.3%). The N-Pt distance ratios and the wing lengths of the three fossil forewings, whose affinity is still questionable (Nos 155, 156 and 157A), fall within the *julius/papuensis* variation range (24.4%/51.4 mm; 26.0%/62.0 mm; 26.1%/52.9 mm). However, in view of the stretched condition of the fossils (extremely in No. 156), it becomes obvious that they must have been considerably shorter in lifetime. Thus, if their "natural" measurements would have been preserved, we would find them within the range of *imperator* variation.

As to the hindwings, there is a non-negligeable overlap between *imperator* and *papuensis*, but none between *imperator* and *julius* ratios: the smaller *julius* specimens (wings shorter than 50 mm) possess N-Pt distance ratios not larger than 31.5%, whereas the large *imperator* and *papuensis* hindwings (longer than 50 mm) have ratios above 32.5%. Unfortunately, the "nearly normally" shaped hindwing No. 185 falls between the variation ranges of *imperator/papuensis* and *julius*, and the N-Pt distance ratio of the extremely stretched hindwing No. 198 cannot be calculated with an acceptable degree of probability. Thus these ratios, in case of the fossil hindwings, do not help to clear the affinities.

The variation ranges in the quantitative venational characters of the three extant species are overlapping to a more or less considerable extent. There are of course some qualitative venation differences between the species. *A. papuensis* is different from the two other species mainly in possessing a triple cell row in the middle of the MP/CuA interspace: a proximally situated paired cell is followed by 2-4 triple cells. None of the fossil hindwings, in which the appropriate part of the wing membrane is preserved (Nos 185, 197A, 198, 1211, 1215, 1219) bears triple cells in the positions indicated. Together with two afrotropical species (*A. tristis*, *A. speratus*) *A. imperator* in the majority of specimens is characterized by a relatively short "anal triangle", especially so in males. Its posterior tip is located anterior to, or at the level of the posterior angle of the anal loop. In all other *Anax* species the "anal triangle", containing 2 cell rows, reaches beyond the angle of the anal loop (as shown by specimen No. 1215 in Fig. 10). Unfortunately, the wing base is preserved in only one of the larger hindwings (No. 198, Fig. 9). Its "anal triangle" shows an *imperator*-like configuration. Summarising this evidence, it should be stated that none of the three large fossil hindwings seems to have affinities with *A. papuensis* and that at least one possesses *imperator*-like structures in its wing base.

The indications presented in favour of *A. imperator*, the only extant species comparable with the five larger fossil wings (distribution, morphometrical and venational references), get a certain support from some hypothetical considerations. The argument to exclude the two other species still involved (*A. julius*, *A. papuensis*) goes as follows:

(1) *A. julius* is the sister species (adelphotaxon), of the westpalearctic *A. parthenope* (PETERS, 1986) and the same most likely holds true for the *papuensis-ephippiger* relation. Due to the mutual apportionment of the apomorphic/plesiomorphic states of several characters between the members in the two species pairs, none of the species can be interpreted as the recently existing "stem species" in relation to the remaining partner. – Compared with *parthenope*, *julius* is apomorphic in having evolved larger eyes, lowered number of Pns and a relatively longer Pt. *A. parthenope* is apomorphic in having changed the green pterothorax colour to purplish brown, in the tendency to express sex differences in some venational characters, not sex-dependent in other species, and by its very high forewing p/a ratios. *A. ephippiger* in relation to *A. papuensis* reached apomorphic stages by elongation and narrowing of T (Tab. I), combined with the loss of division of the basal T-cell into two, and the inwardly orientated first branching of CuA in combination with a strong reduction of the number of double and triple cells in the MP-CuA interspace. In *papuensis*, a short row of triple cells (1-4 in number) in the middle of the MP-CuA interspace, the pronounced expression of the RP_2-bulge and the lowered forewing p/a ratio seem to represent remarkable apomorphic stages.

(2) The members of both pairs are distributed allopatrically; their ranges are nowhere in contact with each other, although the intervening space is occupied by congenerics living elsewhere in sympatry with one of the members of each species pair.

Accepting points (1) and (2), we are forced to acknowledge the consequence: If the species-specific apomorphies have not been evolved as adaptations to a certain set of ecological conditions, the whole area of distribution of each extant pair of sister species never was occupied by one of its partners alone, but partly or at the very best, more or less equal to its recent extension by the stem species. The above explained apomorphies of the four extant species cannot be connected with ecological necessities. *A. julius* and *A. papuensis*, in contrast with *A. parthenope* and *A. ephippiger*, in large segments of their distribution areas exist under tropical-monsoonal conditions, whereas for *papuensis* in southern Australia the climatic circumstances are quite similar to the conditions facing *ephippiger* in southern Africa, and the "life-style" of *julius* in the semi-desert provinces of central China is not very different from the eco-climatic situation important for *parthenope* in Uzbekistan or Turkmenia. Consequently, the species-specific apomorphies of the adelphotaxa most likely evolved within or near their current ranges. If so, there is no reason to believe that *julius* or *papuensis*, at any one time of their history, have been spread into the Mediterranean.

The opposite conjecture would have to claim that, for example, *A. julius* in the Lower Messinian was distributed into Italy and, at some time later, it was there replaced by *parthenope* which, during the Upper Miocene, might have existed elsewhere, but not in Italy. This idea meets the insurmountable difficulty to explain, why - in view of the thus tacitly introduced idea of ecological competition - in our days there is a large zone in southern Asia (India, parts of Indochina), occupied neither by *parthenope* nor by *julius*. The same holds true for the *ephippiger-papuensis* species pair in southeastern Asia.

In Italy, during the Upper Miocene, only *A. parthenope* might have existed (hindwing No. 197A) but not *A. julius*, and only *A. ephippiger* but not *A. papuensis* or - to the contrary - the stem species of one or both of these extant pairs of sister species.

Following this way of reasoning, we have to conclude that the five larger *Anax* wings from the Monte Castellaro site, cannot be connected with *A. julius* or *A. papuensis*. Therefore, *A. imperator* indeed remains the only one species comparable with the larger *Anax* wings Nos 155, 156, 157A, 185 and 198.

The results of our attempts to determine the affinities of the fossil *Anax* wings to extant *Anax* species are summarised in the following identification key. The largely preserved fossil wings (collection numbers in brackets) are placed together with the name of the living species to which they appear to have an individual affinity.

1 Length of forewing 48 mm or more; length of hindwing 46 mm or more 3

1' Forewing shorter than 48 mm; hindwing shorter than 46 mm 2

2 Forewing: length of Pt in % of N-Pt distance length less than 37%, p/a-ratio 76-82%; hindwing: length of Pt in % of wing length 8.6-10.6% .... ***parthenope***

2' Forewing Pt/N-Pt-distance ratio 37-55%, forewing p/a ratio 62-70%; relative Pt length in hindwing 10.5-13.9% .... ***ephippiger*** (Nos 160, 1209A, 1215, 1219)

3 Length of Pt less than 40% of N-Pt distance length in forewing and less than 33% in hindwing 4

3' The indicated relative Pt length ratios exceed 40% in forewing and 33% in hindwing 5

4 In hindwing usually more than 10 antenodals and from 16 to 20 cells along RP_{3-4} down to MA-bifurcation .... ***guttatus*** group, ***nigrofasciatus***

4' 9-12 antenodals (mostly 10) and 13-16 cells along RP_{3-4} in hindwing .... ***parthenope*** (No. 197A)

5 Ratio Pt-length/N-Pt distance length more than 44% in forewing and 38% in hindwing .... ***junius***

5' Same ratio less than 44% in fore- and 38% in hindwing 6

6 Forewing, if longer than 50 mm, with N-Pt distance/wing length ratio exceeding 27.5%; no triple cells in the centre of MP/CuA interspace of hindwing; "anal triangle" not longer than anal loop .... ***imperator*** (Nos 155, 156, 157A, [?]185, 198)

6' Forewing, if longer than 50 mm, with N-Pt distance/wing length ratio 24.5-27.3%; hindwing with triple cells in the centre of MP/CuA-interspace (*A. papuensis* only), "anal triangle" longer than anal loop .... ***julius, papuensis*** ([?] No. 185)

Thus the series of Monte Castellaro *Anax* remnants is composed of wings with affinities to at least three extant species: *A. imperator* (four of five, the questionable specimen being No. 185), *A. parthenope* (one) and *A. ephippiger* (four). Fossils which have been related to one or the other of the two first named species, at present are not distinguishable from living individuals, whereas the wings Nos 160, 1209A, 1215 and 1219, by their wing length comparable with *A. ephippiger* and smaller *parthenope* specimens (but differing from the latter by relative Pt length) possess characters of their own, not seen in *A. ephippiger* nor in its sister species *A. papuensis*.

Due to the impossibility to calculate proportions, the affinities of 13 fragmentary preserved wings cannot be identified. They match the *Anax* diagnosis either by the long 5- to 7-celled T or by the IR_2-"pseudofork", if only the apical part of the wing membrane has been fossilised. Hindwings Nos 1211 and 1217 (proximal parts preserved) each bear a long "anal triangle" (its tip reaches beyond the posterior angle of anal loop) and therefore cannot be related to *A. imperator*. Hypothetically the probability cannot be ruled out that the Monte Castellaro material of *Anax* wings consists of more than 3 species. But due to the lack of diagnostic characters in the fragmented fossils there are no sound arguments in favour of a "more-than-three-species" hypothesis.

As listed in the enumeration of material, the fossil *Anax* wings are supplemented by two fragments of male abdomen with appendices (Nos 210, 211).

No. 210 (Fig. 12a) is preserved by five terminal segments (VI - X), the left upper appendix, the hardly traceable lower appendix and small pieces of the right upper one. On account of the shape of the lower appendix, the fossil has to be assigned to the genus *Anax*. The shape of the left upper appendix seems in conflict with the proposed generic allocation. The appendix is relatively long (5.80-5.85 mm) and narrow (1.1 mm). However, the narrowness, owing to the apparently wanting blade-like broadening, could be an artifact: the badly preserved right upper appendix shows traces of broadening in its middle part as typically for *Anax*. The obliquely cut tip of the appendix ends spineless. Its basal hump is distinctly visible. The deep lateral impressions of the lower appendix are equivalent to the tooth-like protuberances, seen in this position in *Anax imperator*. Segment X is relatively long: 20.7% of the length of segments VII to X taken together (in extant *Anax* specimens the adequate ratio varies from 18 to 20%). Considering the normal *Anax* dimensions of the remaining segments, the lengthening of segment X may be due to a deformation. The dorsal keel along its middle and the clearly indicated amboyment of its hind margin are structures seen in *A. imperator* and *A. parthenope*, but missing in *A. ephippiger* and *A. papuensis*.

The second fossil abdomen (No. 211, Fig. 12b), preserved by seven segments and the full set of appendices, belongs without doubt to the genus *Anax* as apparent from the shape of upper and lower appendix. The upper appendages are broken off near their bases and therefore it was difficult to measure their full length (5.6-6.0 mm). No. 211 possesses no character states, different from the corresponding marks, qualifying *A. imperator* or allowing to distinguish it from No. 210 (save the extended segment X and the uprolled upper appendix of the latter). The combination of characters, relating the two fossils most probably with *Anax imperator*, are given by the tooth-like impressions in the lower appendix and by the spineless tip of the upper appendages.

ANAX CRYPTUS SP. N.

Figures 5-6, 10-11, 14

Material. – 3 forewings [No. 158/A: base, tip and part of posterior border missing; – No. 160 (Fig. 5): nearly completely preserved right wing and basal part of the left wing; – No. 1209A (Fig. 6): completely preserved counterpart]; – 2 hindwings [No. 1215 (Fig. 10): tip and hind margin partly missing; – No. 1219 (Fig. 11): nearly totally preserved]. – **Holotype**: No. 1219, left hindwing of unknown sex allocation (Figs 11, 14).

Type locality. – Monte Castellaro, Marches, Italy.

Age. – Upper Miocene (Lower Messinian). Level "Strato degli insetti"; facies "Marne bituminose"; formation "Gessoso-solfifera".

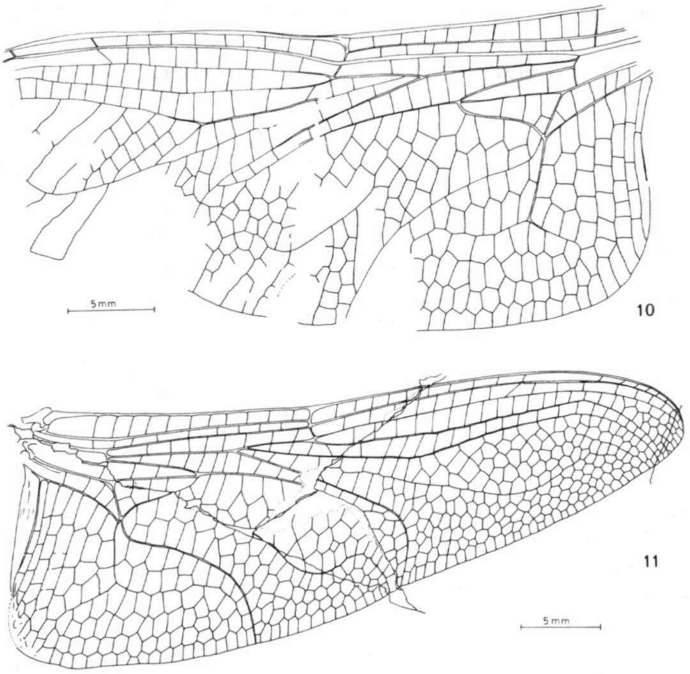
Derivatio nominis. – Until the holotype specimen was excavated in 1991, some fossil remnants in the culminating phase of our investigation referred to the new species, remained hidden among *imperator*-like *Anax* material collected earlier.

DESCRIPTION. – Hindwing of small size (compared with the vast majority of extant species), broadened in its basal section (partly due to deformation by stretching, directed to inner angle of wing membrane), densely reticulated, main veins brownish, Pt and membranule (save its basal part) greyish brown. Character states qualifying the specimen as belonging to the *Anax* group are well expressed. T relatively broad, 5-celled. MP/CuA-interspace proximally with 5 pairs of double cells; CuA without inwardly curved branch. Mspl extremely sinuous; tip of "anal triangle" reaching beyond posterior corner of anal loop. Membranule long and broad.

11 Ans (1 and 5 thickened), 9 Pns; along RP_{3-4} 16 cells before and 6 behind MA/RP_{3-4}-conjunction; 3 crossveins before bridge vein, 2 in supratriangle, 4 cubito-anal crossveins; in one slanting row at maximum 6 cells between IR_2 and Rspl and 5 between MA and Mspl; Pt subtended by 3½ cells; anal loop with 12 cells in 3 rows, "anal triangle" with 9 cells in 2 rows; 7 paranal cells; paranal loop with 11 cells. The whole wing comprises about 595 cells.

Measurements (mm). – Total length 41.4; – width at N 13.4; – maximal width 15.6; – distance between N and proximal end of Pt at wing border 13.4; – Pt length 4.8; – T 5.1 in length (breadth 3.05).

Indices (Tab. I). – The considerably large relative breadth of the wing



Figs 10-11. *Anax cryptus* sp.n., hindwing: (10) paratype, specimen No. 1215; – (11) holotype, specimen No. 1219.

(35.7%) can be explained only partly as resulting from transverse and somewhat inwardly directed stretching of its basal half.

PARATYPES. – (1) Left hindwing No. 1215 (Fig. 10) possesses no substantial differences from the holotype, having an anal loop with 13 and paranal loop with 9 cells, 2 crossveins before bridge vein, but 6 cubito-anal crossveins. Using N--Pt distance and p/a ratio, a wing length of about 42.4-42.9 mm has been calculated (with 44.1 mm being the unlikely upper extreme). Accordingly, the relative breadth varies from 39.8 to 41.1/41.4%; length of Pt 4.7 mm, of T' 5.9 mm. – (2) Right forewing No. 160 (Fig. 5) is preserved in its "natural" shape (possibly slightly stretched in coaxial direction). It bears 17 Ans (1 and 6 thickened), 7 Pns, 3 crossveins in supratriangle and 2 before bridge vein, 17-18 cells along RP_{3-4} down to MA-bifurcation and 5 cells inside T (the proximal cell being divided into 2). There are 6 cells in one oblique row between IR_2 and Rspl and 5 between MA and Mspl (at most); 5 cubito-anal crossveins. Length 47.0 mm, relative breadth 23.1%; length of Pt 4.95 mm, T 6.0 mm. From the left forewing of the same individual only the proximal part (up to the tip of the 5-celled T) was found. – (3) The counterpart of the left forewing No. 1209A (Fig. 6) seems to be pressed in coaxial direction but more obviously (as seen by the undulated hind margin) has suffered from broadening during fossilisation. By its venational characters it is not different from forewing No. 160 save the 6-celled T. Measured length of wing 42.1 mm; Pt 4.35-4.40 mm, T 6.7 mm. – (4) The slightly broadened counterpart of right forewing No. 158A, notwithstanding its incompleteness, belongs to *A. cryptus* sp.n. The low p/a-ratio (63.7%) matches the *ephippiger/papuensis* values. The short N-Pt distance (10.7 mm) indicates a wing length of about 46 mm (in *A. ephippiger* specimens with distance measurements 10.8-11.8 mm have wing lengths 45.1-46.7 mm). As typically for *cryptus* the forewing T bears a divided (double) proximal cell (in *ephippiger* and partly in *papuensis* there is a single one). The specimen bears 17 Ans, 7 Pns, 5 crossveins between the thickened Ans, 3 crossveins in supratriangle and before bridge vein, 5 cubito-anal crossveins, 6-celled T, 5 cells in one row between IR_2 and Ispl and 4 between MA and Mspl.

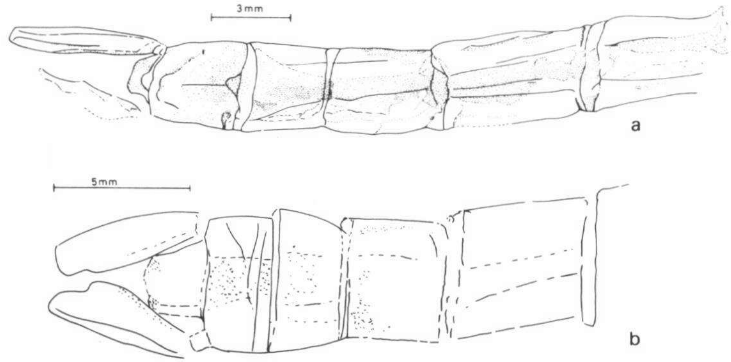


Fig. 12. *Anax* (?) cf. *imperator*, fragments of the abdomen, with ♂ appendages: (a) specimen No. 210; – (b) specimen No. 211.

TAXONOMICAL REMARKS. – Holotype and paratypes of *A. cryptus* sp.n. owing to their relatively small wing length in combination with N-Pt length indices and p/a-ratios (in forewing) have been connected with *A. ephippiger* (cf. above). But in contrast to the fossils with *imperator* or *parthenope* affinites, the wings of *cryptus* are clearly different from those of *ephippiger*. Firstly, the proximal cell in forewing T is divided into two (as to a single one in *ephippiger*). Then there is no inwardly curved branch of CuA in the hindwing (present only in *ephippiger* but lacking in *papuensis*), and there are no triple cells in the centre of the MP/CuA interspace as observable in the two extant species mentioned. The broadening of the MP/CuA-interspace by triple cells (instead of double ones) may be interpreted as an *ephippiger/papuensis* synapomorphy not shared by *cryptus*. The differences between the three species are indicative for the non-confirmable hypothesis that *A. cryptus* sp.n. was the stem species of *papuensis* and *ephippiger*.

ANAX cf. *IMPERATOR* LEACH, 1815

Figures 1-3, 7, 9

Material. – 3 forewings [No. 155 (Fig. 1), No. 156 r (Fig. 2), No. 157A (Fig. 3)], 2 hindwings [No. 185 (Fig. 7), No. 198 (Fig. 9)]. Although undeterminable, No. 156 l, being the fragmentary preserved left wing of specimen No 156 r (right forewing), has to be referred to *A.* cf. *imperator*.

DESCRIPTION. – As pointed out above, the wings listed by their measurements (longer than 50 mm) in relation with some proportions (N-Pt distance ratio of fore- and hindwings, relative length of Pt) as well as some venational peculiarities

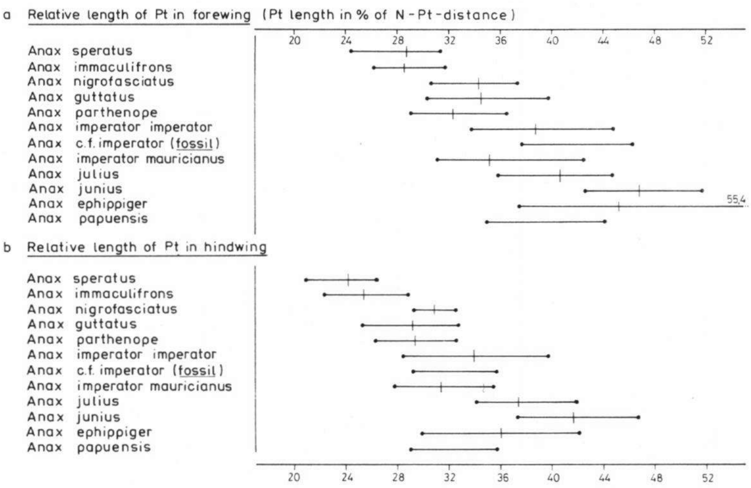


Fig. 13. Diagrams, comparing the relative length of Pt (in % of the distance between N and Pt) of several extant *Anax* species, with the corresponding features of the fossil *Anax* wings.

(structure of MP/CuA interspace, backward extension of "anal triangle" in hindwing) fall within the variation range characterizing *A. imperator* (Tab. I). Overlap of the quantitative parameters of the analysed characters diminishes the likelihood of the identification of the fossils with *A. imperator*. On the account of phylogenetical and distributional considerations, the alternative of identification with *A julius* or *papuensis* is far less acceptable.

In the fossil *imperator*-like forewings there are 16-18 Ans, 7 Pns, 4-5 crossveins between the "primaries", 19 cells along RP_{3-4} down to MA-conjunction with RP_{3-4} (preserved only in No. 157A); the discoidal triangle is 5-celled; length of

Pt 5.9, 6.4 and 5.6 mm.

The *imperator*-like hindwings bear 11 Ans, 9 Pns, 4 crossveins between thickened Ans, 16 cells along RP_{3-4}, four-celled T, 12 and 13 cells inside anal loop, 10 and 11 cells in the paranal loop, and their Pt measures 5.5 and 6.0 mm.

Both abdomens (Nos 210 and 211 [Fig. 12a, b]), looking at their appendices, remain undistinguishable from *A. imperator*. There is no indication of affinity with *A. parthenope*, *julius*, *ephippiger* or *papuensis*. Length of segments VIII--X (taken together) equals 15.5-16.3 mm (No. 210) and 12.9-13.6 mm (No. 211). Compared with the abdomens of *A. imperator* and *ephippiger*, No. 210 seems to be stretched, whereas No. 211 is pressed along axis.

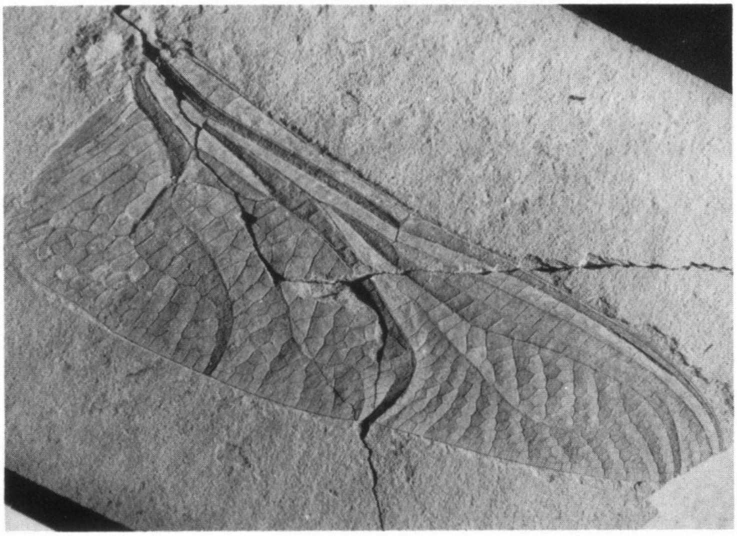


Fig. 14. *Anax cryptus* sp.n., holotype (specimen No. 1219).

ANAX cf. *PARTHENOPE* SELYS, 1839

Figure 8

Material. – 1 left hindwing [No. 197A (Fig. 8)].

DESCRIPTION. – Although preserved only by the frontal and central parts of its wing membrane, the close affinity of the specimen with *A. parthenope* proved traceable. By its low relative length of Pt (29.2% of distance N-Pt) the wing is in agreement with hindwings of *A. parthenope*, *guttatus* and *nigrofasciatus*. But the low number of Ans (10) and cells along RP_{3-4} (15) are not, or rarely seen in the two latter species. Relative length of Pt and p/a ratio of the fossil (106.7%) are much closer to the mean values in *parthenope* than to those in *imperator* or *papuensis*.

The wing possesses 10 Pns, 3 crossveins between thickened Ans, at most 5 cells in one row between RP_2 and Rspl and between MA and Mspl. T 5-celled; 2 crossveins before bridge vein; Pt-length 5.1 mm.

The identification of the specimen with *A. parthenope* has to be understood as the result of a probability calculation. The assumption that the wing may be interpreted as an extreme variant of an *imperator*-like wing is much less likely but cannot be excluded from consideration. No. 197A accentuates the possibility that a *parthenope*-like *Anax* might have been present in the Monte Castellaro odonate fauna.

ANAX SP. INDET.

Due to the scarcity of detectable characters necessary for determination of affinity to one or the other extant species, the following fragmentary wing fossils remained without proper species allocation:

No. **147/147A**: tip of ? forewing and fragment of central portion of the same wing; Pt length 5.4 mm. – No. **154**: basal half of forewing with frontal and backside border missing; T 5-celled. – No. **159A**: counterpart of right forewing, apical third missing, distinctly broadened; 17 Ans, 18 cells along RP_{3-4}, 5 cells between MA and Mspl, 7 inside T; distance 1 Ans - N 17.2 mm. – No. **182**: badly preserved apical third of ? forewing, length of Pt 7.7 mm. – No. **193**: poorly fossilised middle part of left hindwing. – No. **195**: tip of left ? forewing. – No. **1210**: apical half of left forewing, tip missing; 7 Pns, 5 cells between IR_2 and Rspl, length of Pt 4.8 mm, $l_{Pt}/l_{dist.\ N\text{-}Pt}$ 37.9%). – No. **1211**: counterpart of basal half of left hindwing; 9 Ans, 1 and 5 thickened, T 5-celled, anal loop with 13 cells, tip of "anal triangle" reaching beyond posterior angle of anal loop; distance 1 Ans - N 17.2 mm). – No. **1216**: apical third of stretched right hindwing; 7 Pns, 5 cells in one row between IR_2 and Rspl, Pt 5.9 mm, length of Pt in percent of distance N - Pt 37.6%. – No. **1217/1217A**: base of broad right hindwing with small piece of counterpart containing anal loop area; 11 Ans (1 and 5 thickened), T 5-celled, MP/CuA-interspace proximally at least with 4 pairs of cells, 2 crossveins in supratriangle, 4 cubito-anal crossveins, anal loop 11-celled; distance 1 Ans - N 15.4 mm. – No. **1218**: anterior part of left forewing base; more than 10 Ans; T long and narrow, 6-celled.

According to their calculated small wing length (using measurable nodal distances) No. 159A (45-46 mm) and No. 1211 (43-44 mm) may well belong to *A. cryptus*.

AESHNA FABRICIUS, 1775

M a t e r i a l. – 3 right hindwings (part and counterpart No. 169/169A, No. 203/203A, No. 1214/1214A; – basal part of left forewing (part and counterpart No. 161/161A); – fragment of hindwing basal part (No. 1213), apical part of wing (No. 1212); – ♀ abdomen (segments V to X) with appendices (No. 209). – Excluding Nos 1213 and 209 all specimens are fairly well preserved (venation, traces of colour). Difficulties of identification result from missing or badly preserved elements (the bases of the otherwise nearly complete hindwings, outline deformation; cf. Figs 15-17, 19-21).

DIAGNOSIS. – The application of the generic name *Aeshna* to this material means its usage in a mere diagnostical sense. For the purposes of our analysis the genus *Aeshna* will be handled as grasped in the checklist of DAVIES & TOBIN (1985), but following ASKEW (1988) with the addition of *Aeshna isosceles*, not belonging to be bulk of the monophyletically united *Anaciaeschna* species.

Possessing prolonged discoidal triangles in combination with solitary rooted IR_2 and the presence of arched Rspl and Mspl, the fossils are qualified as aeshnids (Aeshnidae). Bearing a true IR-fork in association with 3-5 rows of cells between IR_2 and Rspl as well as between MA and Mspl, and a discoidal field starting with three rows of cells, the hindwings are in agreement with the character pattern of Aeshninae.

Within the Aeshninae, the fossils cannot be identified with any genus of the Gynacanthini and Polycanthagynini for, at least, the following reasons: *Gynacantha, Triacanthagyna, Limnetron, Subaeschna* as well as the *Polycanthagyna* have no or only one proximal double cell between MP and CuA; *Austrogynacantha, Staurophlebia* and *Tetracanthagyna* possess very long discoidal triangles, containing six and even more cells; *Heliaeschna* and *Neuraeschna* possess crossveins in the median space, and in *Agyrtacantha* and *Plattycantha* the IR_2-fork is situated far proximal Pt.

For comparison with the remaining subgroups of the Aeshninae (Aeshnini, *Anaciaeschna*), a certain combination of characters in the fossil hindwings is crucial: (1) symmetrical IR_2-fork with 3-4 rows of cells; – (2) the IR_2-fork situated at or near the level of the proximal end of Pt; – (3) MA-fork with the RP_{3-4}-conjunction of its anterior branch badly defined; – (4) no enlarged cell following that conjunction; – (5) all cells behind it and down to the wing margin are doubled. – The only extant species possessing this full set of characters are the westpalaearctic *Aeshna affinis, isosceles* and *mixta* – with one restriction: in *A. mixta* and *affinis* the MA-RP_{3-4}-conjunction in most cases (70-80% of specimens) is properly expressed. The prolonged membranule (distinctly longer than half of the anal border of hindwing), seen in fossil No. 169 and slightly indicated in No. 203, also belongs to the set of characters of the above three species, as does the feeble bulge of R_2 below Pt (Fig. 4b).

In summary: the fossil hindwings Nos 169, 203 and 1214 represent members of the Aeshnini (within the above defined diagnostical frame), being comparable only with *A. affinis, mixta* and *isosceles*. According to the diagnosis of the remaining fossil remnants listed above, the following remark should be made: All fragments may belong to the genus *Aeshna* and even to one of the species represented by the three well conditioned hindwings, but none of them can be identified with certainty.

COMPARISON. – The excellent condition of the three hindwings, Nos 169, 203 and 1214, enables us to compare the fossils in detail with each other and with the extant species to whom they are similar in the above listed key characters. Inferior to the diagnostic level of these character states there are some remarkable differences between the three fossils as well as between each of them and *A.*

affinis, *isosceles* and *mixta*, favoring the conclusion, that (1) every one hindwing represents a species of its own and that – (2) no one can be identified with any of the extant species. The differences between the three fossil *Aeshna* wings are larger than the dimensions of infraspecific variation known to us from many living aeshnine species.

Table II

Main venational differences between female hindwings of *Aeshna affinis* (Vander L.), *A. isosceles* (Müll.), *A. mixta* Latr., and the fossils *A. messiniana* sp.n. [specimen No. 169], *A. ghiandonii* sp.n. [specimen No. 203], and *A. multicellulata* sp.n. [specimen No. 1214]*

Character	*affinis*	*mixta*	*isosceles*	*messiniana*	*ghiandonii*	*multicellulata*
Pt: relative length	24.7-*27.0*-29.0	19.9-*22.1*-25.0	23.5-*26.9*-30.1	32.8	24.9	27.0
Ans: number	9 -*10.1*-11	8 - *9.4*-11	11 -*12.1*-13	12	12	14
Pns: number	7 - *9.3*-11	8 - *9.4*-13	10 -*11.3*-14	11	13	15
Discoidal triangle: number of cells	2-4 (3 in 56%)	2-5 (5 in 0.4%)	3-5 (5 in 50%)	4	5	5
Doubled cells between MP and CuA in proximal position:						
number of pairs	3 - *4.0*- 5	3 - *4.4*- 5	0-1 (82%), 5-6 (18%)	7	4	11
the same in distal position: number of pairs	none	none	0-5 (2-5 in 36%)	4(5)	none	8(6)
Anal loop: number of cells	6 - *8.3*-11	6 - *7.8*-11	7 - *8.6*- 9	9	12	18
Anal loop: number of cell rows**	2 (2+i in 44%)	2 (2+i in 20%)	3 (2 or 2+i in 36%)	2+i	3	3
Paranal loop present (+) or absent (-)	+ in about 80%	+ in about 95%	+ in about 50%	-	+	+
Cell rows between anal loop and membranule: number	3	3 (2 in 10%)	3 (4 in 23%)	4	3	4
Cells between RP_{3-4} and MA proximal conjunction:						
number	14 -*16.3*-18	14 -*16.7*-19	17 -*18.3*-21	18	19	23
The same distal conjunction: number of cell pairs	2-6	3-8	1-9	7	8	9(10)
Cells in 1 row between IR_2 and Ispl: maximal number	3-4 (4 in 60%)	3-4 (4 in 90%)	3-4 (4 in 15%)	4	4	6
The same between MA and Mspl: maximal number	3-4 (4 in 40%)	3-4 (4 in 95%)	3-4 (4 in 15%)	4	4	6
Distance of IR_2-fork from nodus in % of distance of						
nodus from Pt	87 -*92* -99	77 -*83* -89	84 -*88* -93	82	88	101

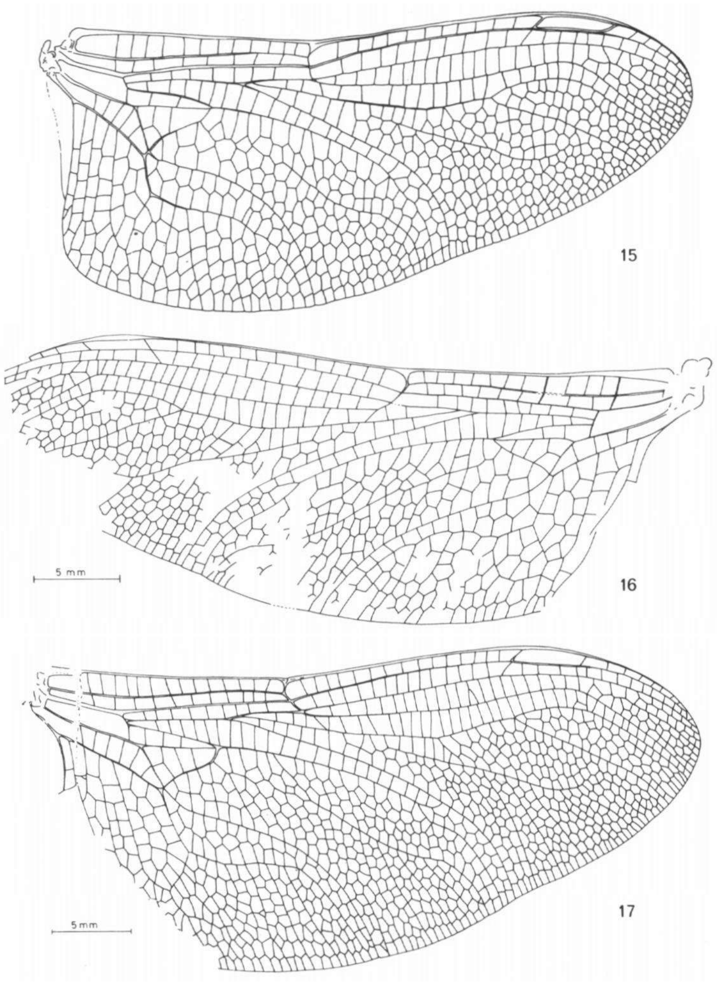
* Quantities are indicated by observed range of variation and *mean value*.

** Single or doubled central cells (intercalary cells) marked by i where present.

With certainty the fossil hindwing No. 1214 (Figs 17, 21) can be considered as a new species, looking at its very dense reticulation (expressed numerically in Tab. II), especially by the excessive numbers of cells in the anal and paranal loops as well as in the space between MP and CuA, and the position of the IR_2--fork, situated at the level of the proximal end of Pt. Having a long row of cell pairs in the CuA/MP interspace, four rows of cells between membranule and anal loop and an evenly running CuA, the specimen offers more signs of affinity with No. 169 and *A. isosceles* than with No. 203 and *A. affinis*/*mixta*.

Hindwing No. 169 (Figs 15, 19) by some of its character states (with some reserve) may be compared with *A. isosceles*: four cell rows between anal loop and membranule and doubled cells in the distal part of the CuA/MP interspace are met with only in a small fraction of *isosceles* specimens (Tab. II), never in *affinis* or *mixta*. Configuration of anal loop (Fig. 15) and large relative length of Pt are unique characters of the specimen. By the relative distance of IR_2--fork from nodus it agrees with *A. mixta*, not with *isosceles* (Tab. II).

Hindwing No. 203A (Fig. 16, 20) offers nearness to *A. mixta* and *affinis*



Figs 15-17. Hindwings of the holotypes of (15) *Aeshna messiniana* sp.n. (specimen No. 169); – (16) *A. ghiandonii* sp.n. (specimen No. 203A); – (17) *A. multicellulata* sp.n. (specimen No. 1214A).

(relative length of Pt, some paired cells between CuA and MP in proximal position, but no pairs in the distal part of that interspace, well developed paranal loop with small number of cells, four cells in one oblique row between IR_2 and Rspl as well as between MA and Mspl), but it cannot be identified with any of the two extant species (Tab. II). The position of the IR_2-fork is in agreement with its location in *A. affinis*; the countings of several cell and crossvein groups, all high in number (Ans, Pns, cells in discoidal triangle and between RP_{3-4} and MA proximal conjunction) meet the upper limit of quantitative variability in *A. mixta*, or even reach beyond (number of cells in the anal loop). Three full rows of cells in the anal loop never have been seen in *mixta* or *affinis*. In only one of 125 *mixta* females a five-celled discoidal triangle and more than 12 (just 13) Pns were noted. In general, hindwing No. 203 possesses, compared with *A. mixta*, a more densely reticulated venation, combined with an *affinis*-like IR_2-fork position.

The shape of the fossil wings at the present state of investigation cannot be taken into account as character of distinctive value. Doubtlessly, the fossils have undergone some change of their dimensions during and after fossilisation. The width/length ratio in all three wings is exceedingly high (38-39% in No. 203, 42-44% in No. 169, 44-45% in No. 1214). Ratios surpassing 33-34% are not known from extant aeshnine. The cells stretched athwart between RP_1 and RP_2 and between RP_2 and IR_2 may serve as an indication of shape modification in the fossil wings after inclosure in the sediment (for comparison see Fig. 18). Nevertheless, relatively broad wings should have been a natural quality of the extinct dragonflies under study. If so, their species-specific status would be reinforced by this character state.

AESHNA MESSINIANA SP. N.

Figures 15, 18-19

Material. – **Holotype** ♀, almost completely preserved right hindwing [No. 169, counterpart No. 169A (Figs 15, 19)].

Type locality. – Monte Castellaro, Marches, Italy.

Age. – Upper Miocene (Lower Messinian. Level "Strato degli insetti", facies "Marne bituminose"; formation "Gessoso-solfifera".

Derivatio nominis. – After the geological age of the holotype.

DESCRIPTION. – Wing medium sized, rather closely reticulated; hyaline with veins brown to dark brown. Wing length a little less than two and one half times of width. Ans 12 (1 and 5 thickened), Pns 11. Pt pale brown, more than five and one half times as long as wide and with distal end strongly oblique. Distance between N and proximal end of Pt about three times the length of Pt. Brace vein moderately oblique and in line with proximal end of Pt. 5 cells below Pt, 7 cells behind it.

Median space of wing free. Sectors of arculus separated at origin. Upper and lower portion of arculus approximately equal in length. Triangle relatively broad, 4-celled. Costal side of triangle as long as distal side and more than one and a half times proximal side. Supratriangle with 2 crossveins and about as long as median space. 5 cubito-anal crossveins (including anal crossing). 6 paranal cells; last two fall within anal loop. Anal crossing above second paranal cell. Anal loop

9-celled, narrow, lengthened to rearward and with tip acute (artifact ?). It is composed of two vertical cell rows with a single pentagonal central cell. Inner side of anal loop twice as long as outer lower side. A paranal loop of unusual configuration (parallel-sided, not closed posteriorly), containing 10 cells, is indicated. One cell row between lower side of the poorly marked paranal loop and wing margin. 4 rows of cells between anal loop and AP. Membranule elongate and extending beyond half of wing base.

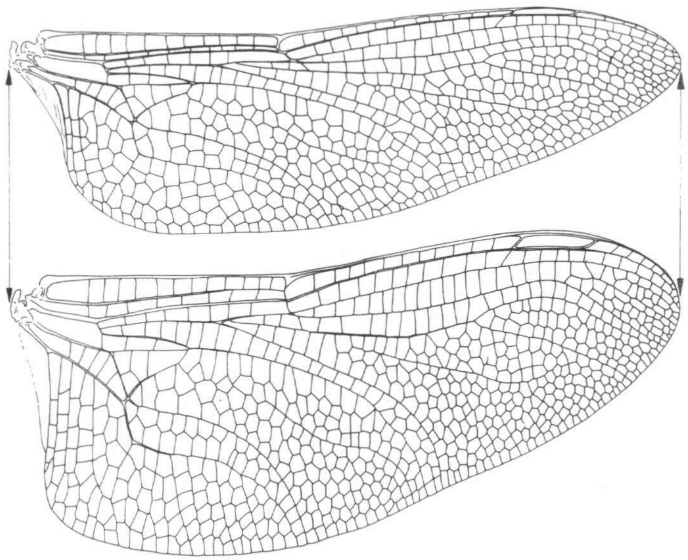


Fig. 18. *Aeshna isosceles* (Müller), ♀, hindwing, projected over the hindwing of the *A. messiniana* sp.n., holotype (specimen No. 169).

CuA evenly running in parallel to MP. 2 rows of pentagonal cells between CuA and MP and 5 single cells distally. Discoidal field beginning with 3 rows of cells and fairly widened distally. Mspl moderately sinuous; between MA and Mspl oblique rows of 3-4 cells. Distal portion of MA without bulge, running parallel to RP_{3-4}. No distinct MA-fork at the beginning of the row of paired cells between MA and RP_{3-4}.

Two bridge crossveins. Portion of bridge beyond N very short. Oblique vein rather close to subnodus. Origin of IR_1 at distal part of Pt. Vein RP_2 bent below median portion of Pt. IR_2 forked about 2 cells proximal to the level of anterior point of Pt. 3-4 cell rows distally between IR_{2a} and IR_{2b} (the two branches of IR_2). Slightly before fork of IR_2 an accessory well-marked fork exists, joining IR_2 with Rspl by a zigzagged line. Rspl deeply concave and subtending a maximum of four cell rows.

Number of marginal cells between RA and RP_1: 3; – RP_1 and IR_1. 3; – IR_1 and RP_2: 5; – RP_2 and IR_{2a}: 1; – IR_{2a} and IR_{2b}: 6; – IR_{2b} and Rspl: 1; – Rspl and $RP_{3\text{-}4}$: 26; – $RP_{3\text{-}4}$ and MA: 2; – MA and Mspl: 2; – Mspl and MP: 11; – MP and CuA: 1; – CuA and AP: 29. The whole wing comprises 758 cells.

Measurements (mm). – Wing length 39.3; – width at nodus 16; – distance from wing base to nodus 16; – distance from nodus to apex 22.9; – distance from nodus to proximal end of Pt 13.2; – Pt length 4.6 mm, its width 0.8; – triangle 4.6 (costal side), 2.7 (proximal side), 4.6 (distal side).

AESHNA GHIANDONII SP. N.

Figures 16, 20

Material. – **Holotype** ♀, in its counterpart relatively well preserved right hindwing [No. 203, counterpart No. 203A (figs 16, 20)].

Type locality. – Monte Castellaro, Marches, Italy.

Age. – Upper Miocene (Lower Messinian); the specimen was recovered from a layer underlying the "Strato degli insetti", facies "marne bituminose"; formation "Gessoso-solfifera".

Derivatio nominis. – Named after the friend of the first author, Mr Alberto Ghiandoni, of Pesaro, amateur paleontologist.

DESCRIPTION. – Wing medium sized, reticulation relatively dense; hyaline with veins dark brown to black. Ans 12, (1 and 5 thickened), Pns 13. Pt brown, narrow, about five times as long as wide and subtending 3½ cells. Distance between N and proximal end of Pt about four times Pt length. Median space free. Arculus situated between first and second antenodal, but much nearer to the second. Triangle 5-celled; costal side about twice proximal side. Supratriangle with 2 crossveins, slightly longer than midbasal space. 4 cubito-anal crossveins. 6 paranal cells; last three fall within anal loop. Anal crossing above the second paranal cell. Anal loop elongate with tip acute and 12-celled; composed of 3 vertical cell rows with a single central cell, octagonal in shape. Paranal loop distinctly marked, 7-celled. 3 rows of cells between anal loop and AP. Membranule badly preserved. Between MP and CuA 2 cell rows in proximal position.

Discoidal field with 3 rows of cells; a maximum of 4 cell rows between MA and Mspl. Mspl slightly curved. 2 rows of cells distally between MA and $RP_{3\text{-}4}$, running almost parallel. No distinct MA-$RP_{3\text{-}4}$ conjunction.

Two bridge crossveins. Oblique vein close to subnodus. IR_1 originates at distal end of Pt. RP_2 slightly bent below distal part of Pt. Fork of IR_2 situated well before proximal side of Pt; it includes 4 cell rows. Rspl curved inwards below Pt, subtending at maximum 4 rows of cells. Tip of wing missing.

Due to fossilisation of a somewhat damaged wing, countings of its cell numbers on the whole are impossible. Sets of marginal cells are preserved between $RP_{3\text{-}4}$ and MA (2), MA and Mspl (1) and MP and CuA (2). The unviolated specimen would comprise about 680-700 cells.

Measurements (mm). – wing length 36.8 (preserved part); – width at N 13.5; – distance between N and proximal end of Pt 14; – Pt length 3.4, width 0.7 mm; – triangle 4.1 (costal side), 2.1 (proximal side), 3.4 (distal side).

AESHNA MULTICELLULATA SP. N.

Figures 17, 21

Material. – **Holotype** ♀, in the counterpart well preserved left hindwing, but anal margin missing [Nos 1214A and 1214 (Figs 17, 21)].

Type locality. – Monte Castellaro, Marches, Italy.

Age. – Upper Miocene (Lower Messinian). Level "Strato degli insetti"; facies "Marne bituminose"; formation "Gessoso-solfifera".

Derivatio nominis. – Named after the very dense reticulation of the wing membrane, which is responsible for the exceedingly large number of cells in this species.

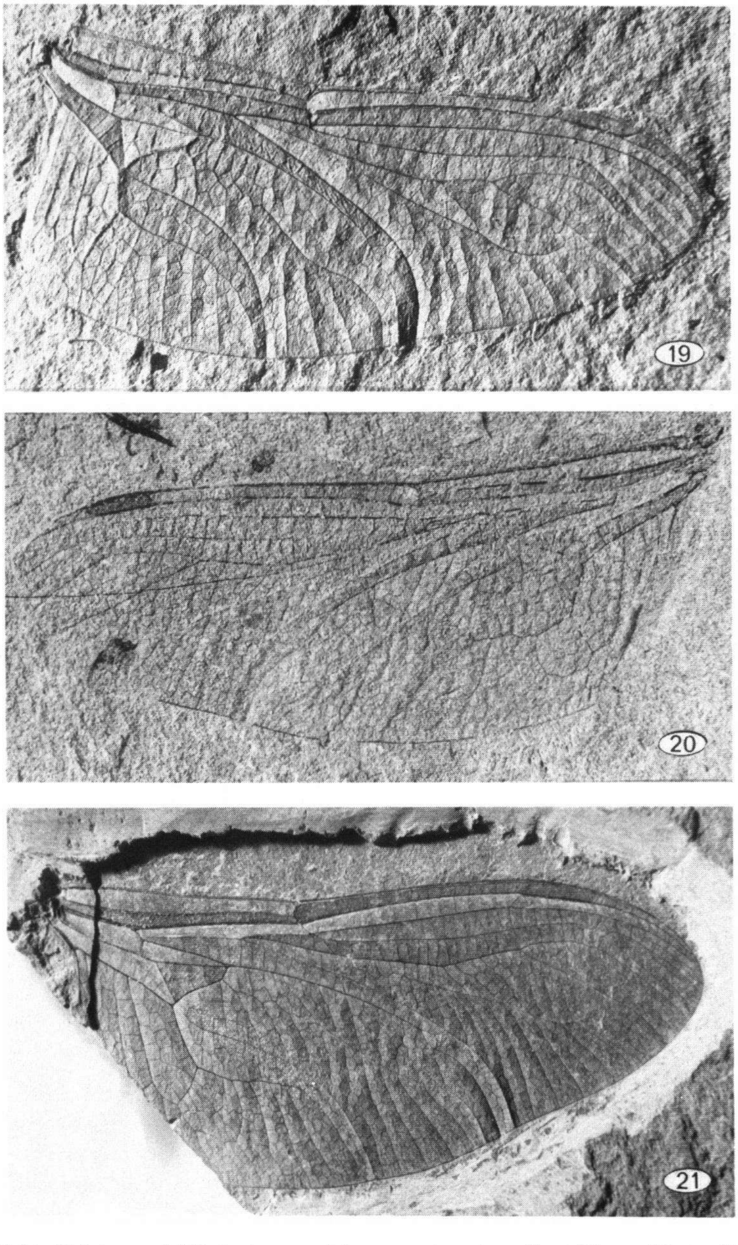
DESCRIPTION. – Medium sized hindwing, very densely reticulated in all of its parts, hyaline. Length of wing exceeds its width distinctly less than two and a half times. Ans 14 (1 and 7 thickened), Pns 15. Pt pale yellow to pale brown, its distance from N about three and half times of its length. Brace vein in line with proximal flank of Pt. 4 cells below and 8 behind Pt.

Median space free. Arculus situated between second and third antenodals. Sectors of arculus well separated, its upper and lower portion equal in length. Triangle broad (proximal side more than half as long as costal side) and 5-celled. Supratriangle with five crossveins. 7 paranal cells, last 3 fall within anal loop. Anal crossing between second and third paranal cell. Anal loop very long, containing 18 cells in 3 rows. Paranal loop well developed, large, with 21 cells. 4 rows of cells between anal loop and AP. The extension of membranule not preserved.

The interspace between MP and evenly running CuA very broad in its proximal part, covered throughout by a double row of cells, starting and interrupted twice by juxtaposition of 3 cells and near its midst by a single cell. Discoidal field beginning with 4 rows of cells. Mspl slightly sinuous. Between MA and Mspl 5 (at maximum 6) cells in poorly marked oblique rows. Anterior branch of MA-bifurcation meets RP_{3-4}, but the bulging of its posterior branch weekly expressed. Double row of cells distal of MA-bifurcation complete down to wing margin.

Three bridge crossveins; oblique vein close to subnodus. Origin of IR_1 beyond distal end of Pt. RP_2 blandly bent below distal portion of Pt (the curvature being marked only by one double cell between RP_2 and IR_{2a}). IR_2-fork situated at the level of anterior flank of Pt. 4 rows of cells between its branches. Rspl deeply concave, subtending up to 6 cells in oblique rows.

Number of marginal cells between RA and RP_1: 2; – between RP_1 and IR_1: 3; – IR_1 and RP_2: 4; – RP_2 and IR_{2a}: 1; – IR_{2a} and IR_{2b}: 6; – IR_{2b} and Rspl: 1; – Rspl and RP_{3-4}: 29; – RP_{3-4} and MA: 2; – MA and Mspl: 2; – Mspl



Figs 19-21. Holotypes of (19) *Aeshna messiniana* sp.n. (specimen No. 169); – (20) *A. ghiandonii* sp.n. (specimen No. 203A); – (21) *A. multicellulata* sp.n. (specimen No. 1214A).

and MP: 16; – MP and CuA: 1; – CuA and AP: (not preserved). The whole wing would comprise about or a little more than 1.000 cells.

Measurements (mm). – Wing length 42.5; – width at N 19.0; – distance from wing base to N 15.8; – distance between N and proximal tip of Pt 4.3; – its width 1.05; – triangle 4.7 (costal side), 3.0 (proximal side), 4.2 (distal side).

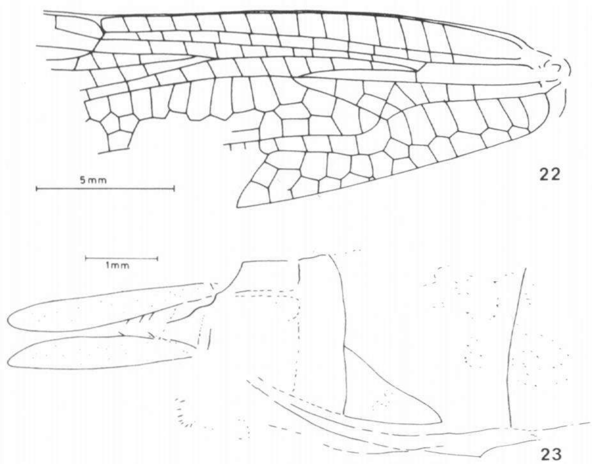
AESHNA SP. INDET.

Figures 22-23

Material. – No. 161/161A (part and counterpart): basal part of left forewing; No. 1212: apical part of wing; No. 1213: fragment of hindwing (basal part); No. 209: female abdomen (segments V to X) with appendices.

As to locality and age all fragments belong to the complex of specimens we are dealing with in this paper. None of these fragmentary fossils can be assigned to one of the three above described new species with sufficient certainty.

Forewing No. **161** (Fig. 22) with 14 Ans (1 and 5 are "primaries"), 4-celled discoidal triangle, divided subtriangle (5 cubital crossveins, including anal crossing), 3 bridge crossveins, 7 paranal cells and discoidal space, starting with 3 rows of cells. Median space without crossveins. Crossveins in supratriangle missing or (more likely) not preserved. Possessing a low number of paranal cells and cubital crossveins as well as a 4-celled discoidal triangle; the fragment, 18.8 mm in length, cannot be compared with *A. isosceles* and therefore even less with *A. messiniana* sp.n. or *A. multicellulata* sp.n., bearing still more cells and crossveins. On the other hand, the specimen offers nearness to *A. mixta*/*affinis*. Leaving aside the question of crossveins in supratriangle, it shows clear affinities to *A. mixta* (in *affinis* forewings the discoidal triangle is mostly only 3-celled, the subtriangle very rarely divided) and therefore the forewing fragment in question may well belong to *A. ghiandonii* sp.n. The nearness of the arculus segments in the forewing of No. 161 contrasting with the picture



Figs 22-23. *Aeshna* sp. indet: (22) forewing fragment of specimen No. 161; – (23) ♀ abdomen of specimen No. 209.

in the *ghiandonii* hindwing does not matter: in all the aeshnine the distance between arculus sectors is higher in hind- than in forewing.

It is impossible to say whether the distal part of wing No. **1212** is a fore- or a hindwing fragment. Position of the IR_2-fork as well as the lowered numbers of cells in the areas preserved (inside IR_2-fork, between IR_2 and Rspl, between Rspl and wing margin) are similar with the character states of *A. messiniana* sp.n. and *A. ghiandonii* sp.n., but different from the picture possessed by *A. multicellulata* sp.n. By the coloration of Pt and crossveins (brown, longitudinal veins dark brown), the beginning of IR_2 (below distal part of Pt) and the number of cells below Pt (3½) the fragment comes nearer to *ghiandonii* (No. 203) than to *messiniana* (No. 169).

Hindwing fragment No. **1213** is poorly preserved. its 4-celled discoidal triangle, being relatively broad (length of proximal side equals about 65% of its anterior length), resembles the triangles of *messiniana* and *multicellulata* (with corresponding ratios 62 and 61%) more than that of *ghiandonii* (52%).

Details of the posterior part of the female abdomen (No. **209**, Fig. 23) are badly visible (borders of segments, basal parts of appendices, ovipositor). The blackish coloured appendices, about 2.7 mm in length and 0.43-0.45 mm broad, are relatively short. Their relative length equals 38-42% of the length of segments VIII, IX and X taken together, thus being near the value of the adequate ratio in *isosceles* females (40-48%). The corresponding ratios of the remaining extant species, with which the fossils have been compared are: *Aeshna affinis* 48-52%, *A. mixta* 65-79%, and *Anax imperator* 51-61%.

CONCLUDING REMARKS

Looking at the material presented in this paper it becoms obvious that the Upper Miocene has to be considered as in important period in the formation of the westpalaearctic aeshnid assemblage. Some species of the present day fauna, such as *Anax imperator* and, perhaps *A. parthenope*, already existed, while other members of the Lower Messinian fauna (*Aeshna multicellulata*) disappeared and did not survive until Holocene times. *Anax cryptus* and the two remaining Monte Castellaro *Aeshna* species may be interpreted as ancestral morphotypes of *Anax ephippiger/papuensis*, *Aeshna isosceles* (*A. messiniana*) and the *A. mixta/affinis* sister species group, respectively (*A. ghiandonii*), thus indicating the starting course of evolution of five extant aeshnid species.

But the shakiness of this conjecture should be emphasized strongly. The morphological nearness of the fossils in question to the mentioned extant species does not document phylogenetical relationships until uncontradicted synapomorphies have been traced. As to the *Aeshna* species, appropriate analyses of certain character states (configuration and positions of IR_2-fork, MA-RP_{3-4}-conjunction, anal loop, cells between MP and CuA, extension of membranule etc.) still have to be performed. Preliminary studies have shown that multiple parallelism in the apomorphic trends of character transformation at genus and species level is realized with considerable frequency. In order to overcome this phenomenon, a comparitive examination of all existing groups of aeshnids is required. Another reason for postponement of phylogenetical speculations is given by the absence of male *Aeshna* specimens in the fossil material at hand. Knowledge of the structure of the anal triangle in the male hindwing, of the second abdominal segment and appendices would seriously increase the possibilities of offering a testable hypothesis on the relationships of the species concerned.

ACKNOWLEDGEMENTS

We feel much obliged to T. BATTIN (Vienna) for the loan of *Anax immaculifrons* specimens and to H.M. ANDRE (Musée Royal de l'Afrique Centrale, Tervuren), who mailed material of Central African aeshnids for determination to the second author, which contains good series of *Anax imperator mauricianus* and *A. speratus*, thus essentially improving the solidity of our comparisons, mainly based on the collections of the Zoological Museum, Berlin (curator K.K. Günther).

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