

Stadia and growth ratios of Odonata: a review¹

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Received 17 August 2001; revised and accepted 24 October 2001.

Key words: Odonata, dragonfly, stadia, ecdysis, growth, review, terminology.

Abstract

A terminology is presented for structures and events in larval development of Odonata with the aim of bringing terms into conformity with those used for other insect orders in the light of accepted views of homology. The terms 'exuvia', 'larva', 'prolarva' and 'stadium' receive special mention. Records of the number of stadia required to complete larval development for 118 species are listed and analysed, showing that the range for Odonata is 8 through 18 stadia (8 through 18 for 8 species of Anisoptera; 8 through 17 for 38 species of Zygoptera) averaging 12.4 stadia for the order (Anisoptera 12.5 and Zygoptera 12.2), in which >90% of records range from 10 through 16 stadia (both Anisoptera and Zygoptera >90%). The number of stadia varies between and within species, sometimes within members arising from a single egg batch. No unifying hypothesis exists to rationalize variation in the number of stadia. Duration of successive stadia within a species can be a smooth, increasing progression but can also show wide departures from such a pattern. Duration of a single stadium can range from 1 day (or <1 day in the prolarva) through >1 year. Uniformity of size of the final-stadium larva can be achieved by the growth ratio (between successive ecdyses) compensating for the number of stadia. Aeshnidae typically have more stadia than do Libellulidae and also have a smaller average growth ratio. Ontogenetic profiles of growth ratios for different dimensions tend to have a characteristic form for each dimension, regardless of the eventual number of stadia. For some dimensions (e.g. headwidth) and some species the profile forms a smooth declining progression but for others (e.g. length of caudal appendage) it fluctuates irregularly. Headwidth therefore represents the dimension of choice for specifying stages of larval development. Rewarding avenues for research include the documentation of prospective links between larval life style on the one hand and stadal numbers and growth-ratio profiles on the other, and discovery of morphological characters that make it possible to determine to species larvae of early stadia.

¹ This paper has been invited by the International Journal of Odonatology.

Introduction

Postembryonic development of Odonata, namely the pattern of larval growth, has been relatively poorly studied and yet has the potential to yield valuable insights for our understanding of voltinism and seasonal regulation, as well as to provide information needed for the identification to species of early stadia – a prerequisite for research on larval ecology to proceed in a balanced way.

Before reviewing questions that await answers, I address the matter of terminology.

Full scientific names of all species, if not in the text, are given in Table 2.

Terminology

The morphology and development of larval Odonata have suffered disproportionately from arbitrary and inconsistent terminology. Odonatologists owe it to the standing of their discipline to ensure that, as far as possible, the terminology they adopt conforms with prevailing interpretations of homology derived from other insect orders. As a contribution to this much-needed reform, I list in Table 1 terms which I regard as appropriate in that they are unambiguous and comply with those in current use for other insect orders. In presenting this list, I am assuming that odonatologists who publish their work see merit in using terms whose meaning is unequivocal and that are in current use internationally.

Among the terms defined in Table 1, some deserve further comment.

Exuvia

The Latin word ‘*exuviae*’ (1st declension, feminine), meaning cast-off clothing, exists only in the plural form (see Tillyard 1917: 378). Being aware of this, but also of the practical need to have a singular form, certain authors have recognised the singular noun ‘*exuvia*’ (conforming in declension and gender to ‘*exuviae*’) to serve this purpose (Calvert 1929: 233; Corbet 1957: 33). French-, German-, and Italian-speaking odonatologists do not encounter this need because they have changed the Latin word into a French or German one that has a singular form. If, as seems likely, English-speaking authors continue to use the Latin word, they should either recognise the recommended singular term ‘*exuvia*’ or else commit the solecism of using a plural word in a singular sense, thus also losing precision of meaning. ‘*Exuvium*’, a fanciful construct found in some glossaries, is clearly inadmissible.

Larva

Some authors, apparently wishing to emphasise the fact that Odonata belong to the Hemimetabola (Exopterygota), have used terms such as ‘*nymph*’ and ‘*naiad*’. Neither term has contemporary merit. The former was coined by early French entomologists to mean either the pupa of certain orders of holometabolous (endopterygote) insects (e.g. Lyonet 1832: plate 11) or the later stadia of Odonata in which the wing sheaths

Table 1. A terminology for structures and processes in the postembryonic development of Odonata.

Appropriate term	Meaning and remarks
aestivation	Reduction of biological activity, in direct response to conditions unfavourable for uninterrupted development, during the summer in a temperate climate.
aestivohibernation	Reduction of biological activity, in direct response to conditions unfavourable for uninterrupted development, during the summer and succeeding winter in a temperate climate.
apolysis	Separation of the new cuticle from the old cuticle before ecdysis, marking the beginning of the pharate condition in the moulting cycle (see Hinton 1946; Jones 1978).
bivoltine	Completing two generations in a year.
cohort-splitting	Fragmentation of a year group (cohort) of larvae into two or more components that differ in growth rate and typically subsequently in voltinism.
diapause	State of suspended development that may supervene at some stage or stages in the life cycle and that typically constitutes an anticipatory response to conditions unfavourable for uninterrupted development (see Andrewartha 1952; Danks 1987).
ecdysis	Moulting; the shedding of the outer skin or cuticle (cf. apolysis) (see Hinton 1946; Jones 1978).
emergence	Events associated with ecdysis from larva to adult.
exuvia	Plural exuviae . Outer skin shed during ecdysis. For explanation see text.
F-0	Designation for final larval stadium, preceded by the penultimate (F-1), antepenultimate (F-2) stadia and so on. Equivalent to 'F' (e.g. Norling 1984) and 'Z' (e.g. Bilek 1962; Norling 1971) of some authors. F-0 is preferred because the symbols 'F' and 'Z' can have other meanings.
growth ratio	(GR). ('Taux de croissance'; 'Wachstumsfaktor'). The proportionate change in size of a specified part of the body during and immediately after ecdysis (Wigglesworth 1972: 61; Cole 1980).
hibernation	Reduction of biological activity, in direct response to conditions unfavourable for uninterrupted development, during the winter in a temperate climate.
instar	Stage of morphological development between two successive apolyses. Not equivalent to stadium (see text).
labial suture	Flexible articulation between the prementum and the postmentum (see Corbet 1953).
labium	Fused second maxillae, specialized in the larva to form a prehensile organ that can be protracted suddenly during prey capture. Sometimes termed 'mask'.
larva	Developmental stage between egg and adult (see text).
metamorphosis	Changes in morphology, physiology and behaviour that take place during the transition from the last larval stadium to the adult. The vernacular term 'metamorph' has sometimes (inappropriately) been coined (without definition), apparently to denote an individual in the act of emergence.
multivoltine	Completing more than three generations in a year.
partivoltine	Completing a generation in more than two years.
pharate	Condition in which, before ecdysis, the new cuticle has become separated from the old cuticle (cf. apolysis) (see Hinton 1946; Jones 1978).

Table 1. Continued.

Appropriate term	Meaning and remarks
postmentum	Unpaired segment of the larval labium proximal to the labial suture (cf. prementum) (see Corbet 1953).
prolarva	First, usually very abbreviated, larval stadium (see text).
seasonal regulation	Array of responses whereby each developmental stage tends to be confined to a particular season.
semivoltine	Completing a generation in two years.
siccation	Reduction of biological activity, in direct response to conditions unfavourable for uninterrupted development, during the dry season in a tropical climate (see Corbet 1999: 261).
spring species	Species that habitually spends the last winter before emergence as a F-0 larva (typically in diapause) and consequently typically emerges synchronously and early in the year (cf. summer species) (see Corbet 1954).
stadium	Stage of morphological development between two successive ecdyses. Not equivalent to instar (see text).
summer species	Species that habitually spends the last winter before emergence in a stadium before F-0 and consequently typically emerges later and with less synchronisation than spring species (q.v.) (see Corbet 1954).
supernumerary F-1	Stadium possessing morphological characters intermediate between those of F-1 and F-0 (see text).
teneral	Condition (of a larva or adult) after and within 24 hours of ecdysis, when the exocuticle is almost colourless and still unsclerotised. The teneral stage is by definition brief (see Conrad & Herman 1990) and thus not equivalent in adults to the prereproductive period – a much longer phase that precedes the attainment of sexual maturity.
thanatosis	Reflex immobilisation, sometimes termed 'death feigning'.
trivoltine	Completing three generations in a year.
univoltine	Completing one generation in a year.
voltinism	The number of generations completed in a year.
wing sheaths	Outer covering of wing rudiments visible externally from about stadium F-6 onwards. Sometimes termed 'buds' or 'pads', both of which words have other meanings in different contexts.
winter critical size	Size in autumn above which a larva is stimulated to develop rapidly so that metamorphosis (followed by emergence) will take place the next spring, and below which a larva will be induced to enter diapause the next spring, thus postponing emergence for an additional year (see Norling 1984: 148). Usually coinciding with the winter frequency minimum .

are visible (e.g. Réaumur 1742: 391; Lyonet 1832: plate 18, 562). The latter term ('naiad'), apparently introduced without explanation by Lucas (1930), is an idiosyncratic oddity that can safely be abandoned. Although Tillyard (1917: 6, 7), a distinguished comparative morphologist, argued against using the term 'nymph' for larval Odonata, it has nevertheless often been used, especially in North America, during the 20th Century. The term's demise now appears to have been confirmed by formal adoption of the term 'larva' in two standard text books on North American Odonata (Westfall & May 1996: 3; Needham et al. 2000).

Prolarva

Published records of the number of stadia are sometimes ambiguous because some authors (about 37% so far, to judge from the records in Table 2) treat the prolarva as the first stadium whereas others do not. This represents a curious anomaly because expert opinion, with few exceptions (e.g. Ross 1967: 173), is united in regarding the prolarva as a true stadium. Thus Richards & Davies (1977: 355) observe that "In most exopterygotes, the Neuroptera and Trichoptera, the insect that emerges from the egg is enclosed in the so-called embryonic cuticle which is either shed during eclosion so that it remains behind in the egg-shell or is cast shortly after hatching is complete, the insect bearing it being variously known as the pronymph (Odonata), vermiform larva (Acrididae) or primary larva (Cicadidae). There seems little doubt that this stage represents a greatly abbreviated first instar... though it is usually excluded from the system of numbering the instars in life-cycle studies." Elsewhere (p. 503) these authors state that the prolarva moults to yield the second-stadium larva. Likewise Tillyard (1917: 69) explicitly dismisses the claim that the prolarval sheath is the amniotic covering, emphasising that the sheath is non-cellular and chitinous, and concluding: "It seems clear that the pronymph is really the first larval instar, and its sheath just an ordinary cuticle, such as is cast at ecdysis." Other authors who hold his view on grounds of comparative morphology include Grieve (1937: 124) and Jones (1978). Indeed, I have encountered no evidence for the alternative view (that the prolarva is *not* the first stadium), although some authors rationalize their adoption of this usage on the sole grounds that to do so is customary. Thus Kormondy (1959: 46), though persuaded that the prolarva represents the first instar, elects to discount it as an instar "to conform to established usage". Similarly Sternberg & Buchwald (1999: 98) recommend not including the prolarva when numbering larval stadia because to do so is "not customary". Such approaches ensure that an unsupportable practice becomes self-perpetuating, despite being contrary to the tenets of comparative morphology. With these considerations in mind, one may hope that the status of the prolarva as the first larval stadium will now be generally recognised and henceforth be adopted in accounts of larval stadia. Nevertheless, because published accounts have lacked consistency in this regard, it will always be necessary to state whether or not the prolarva is included in the total stadal number.

Table 2. Published records of number of stadia required to complete larval development in Odonata.

Species ¹	n ²	No. stadia ³	Average	Reference
ANISOPTERA				
Aeshnidae				
<i>Aeshna bonariensis</i> Rambur	1	12 ⁴		Rodriguez Capitulo (1980)
<i>Aeshna caerulea</i> (Ström)	50	14, 16 ⁴	14.1	Sternberg (1990: 71)
<i>Aeshna cyanea</i> (Müller)	170	11-14 ⁴	12.1	Schaller (1960)
<i>Aeshna juncea</i> (Linnaeus)	55	17, 18 ⁴	17.3	Sternberg (1990: 77)
<i>Aeshna mixta</i> (Latreille)	71	10-12 ⁴	10.3	Schaller & Mouze (1970)
<i>Aeshna subarctica elisabethae</i> Djakonov	34	15-17 ⁴	17.1	Sternberg (1990: 82)
<i>Aeshna tuberculifera</i> Walker	4	14-16 ⁴	14.0	Lincoln (1940)
<i>Aeshna viridis</i> Eversmann	?	12 ⁴		Münchberg (1930b)
<i>Anax imperator</i> Leach	30	15 ⁴		Melzer (1996)
<i>Anax junius</i> (Drury)	33	10-13 ⁴	11.8	Beesley (1972: 35)
<i>Anax panybeus</i> Hagen	several	13 ⁴		Obana & Inoue (1972)
<i>Anax papuensis</i> (Burmeister)	many	16 ⁵		Hawking & New (1996)
<i>Coryphaeschna perrensi</i> (McLachlan)	5	16 ⁴		Carvalho (1992)
<i>Nasiaeschna pentacantha</i> (Rambur)	8	14, 15	14.5	Dunkle (1985)
Cordulegastridae				
<i>Cordulegaster bidentata</i> Selys	many	15 ⁴		Dombrowski (1989)
<i>Cordulegaster boltonii</i> (Donovan)	many	14 ⁴		Pfuhl (1994)
Corduliidae				
<i>Cordulia aenea aenea</i> (Linnaeus)	?	12 ⁴		Robert (1958: 328)
<i>Cordulia aenea amurensis</i> Selys	many	13 ⁵		Ubukata (1980)
<i>Epitheca bimaculata bimaculata</i> (Charpentier)	2	12, 13	12.5	Bilek (1961)
<i>Epitheca bimaculata sibirica</i> Selys	4	14 ⁴		Sonehara (1968)
<i>Epitheca canis</i> McLachlan	1	14 ⁴		Kormondy (1959)
<i>Epitheca cynosura</i> (Say)	1	13 ⁴		Kormondy (1959)
<i>Epitheca marginata</i> (Selys)	1	13 ⁴		Sonehara (1982: 149)
<i>Epitheca spinigera</i> (Selys)	1	13 ⁴		Kormondy (1959)
<i>Procordulia artemis</i> Lieftinck	many	15 ⁴		Lieftinck (1933)
<i>Somatochlora alpestris</i> (Selys)	118	12-14 ⁴	13.5	Sternberg (1990: 59)
<i>Somatochlora arctica</i> (Zetterstedt)	31	12 ⁴		Sternberg (1990: 62)
<i>Somatochlora filosa</i> (Hagen)	3	13		Dunkle (1977)
<i>Somatochlora metallica</i> (Vander Linden)	?	13 ⁴		Münchberg (1932)
<i>Somatochlora viridiaenea viridiaenea</i> Uhler	8	13 ⁴		Miyakawa (1971)
Epiophlebiidae				
<i>Epiophlebia superstes</i> (Selys)	?	15 ⁴		See Asahina (1954: 141)
Gomphidae				
<i>Asiagomphus pryeri</i> (Selys)	several	15		Aoki (1994)
<i>Gomphus flavipes flavipes</i> (Charpentier)	several	15 ^{4,6}		Müller (1995)
<i>Gomphus pulchellus</i> (Selys)	several	11 ^{4,6}		Suhling & Müller (1996)
<i>Gomphus vulgatissimus</i> (Linnaeus)	several	15 ^{4,6}		Müller (1995)

Table 2. Continued.

Species ¹	n ²	No. stadia ³	Average	Reference
<i>Hemigomphus gouldii</i> (Selys)	several	16 ³		Hawking & New (1996)
<i>Ictinogomphus rapax</i> (Rambur)	2	12		Begum et al. (1980)
<i>Onychogomphus uncutus</i> (Charpentier)	several	12-14 ^{4,6}	13	Schütte et al. (1998)
Libellulidae				
<i>Brachythemis contaminata</i> (Fabricius)	several	11, 12	11.5	Mathavan (1990)
<i>Braclonopyga geminata</i> (Rambur)	1	13		Kumar (1973)
<i>Crocothemis erythraea</i> (Brullé)	1	8 ⁴		Wenger (1955)
<i>Crocothemis servilia</i> (Drury)	several	10		Begum et al. (1985)
<i>Diplacodes bipunctata</i> (Brauer)	several	13		Rowe (1992)
<i>Diplacodes haematodes</i> (Burmeister)	many	14 ⁵		Hawking & New (1996)
<i>Diplacodes trivialis</i> (Rambur)	9	12		Pandian & Mathavan (1974)
<i>Erythemis attala</i> (Selys)	many	14 ^{4,5}		Rodrigues Capitulo (2000)
<i>Erythemis simplicicollis</i> (Say)	1	14 ⁴		Bick (1941)
<i>Hadrothemis camarensis</i> (Kirby)	several	13 ⁵		Copeland et al. (1996)
<i>Leucorrhinia dubia</i> (Vander Linden)	61	14 ⁴		Sternberg (1990: 66)
<i>Libellula depressa</i> Linnaeus	3	11, 13	12.3	Gardner (1953)
<i>Libellula julia</i> Uhler	57	13-16 ⁴	14.5	Desforges & Pilon (1989)
<i>Libellula quadrimaculata</i> Linnaeus	?	11		Gardner (1951)
<i>Microthemis pachygastra</i> (Selys)	several	11, 12 ⁴	11.5	Miyakawa (1970)
<i>Microthemis bella</i> (Uhler)	4	12, 13 ⁴	12.3	Calvert (1929)
<i>Microthemis tullia tullia</i> (Drury)	2	9		Begum et al. (1990b)
<i>Orthetrum albistylum</i> (Selys)	8	13 ⁴		Bilek (1962)
<i>Orthetrum brunneum</i> (Fonscolombe)	several	14 ⁵		Kumar (1971)
<i>Orthetrum caledonicum</i> (Brauer)	many	15 ⁵		Hawking & New (1996)
<i>Orthetrum cancellatum</i> (Linnaeus)	many	12 ^{1,6}		Katzur (1998)
<i>Orthetrum pruinatum neglectum</i> (Rambur)	2	10		Kumar (1970)
<i>Orthetrum sabina sabina</i> (Drury)	several	14, 15	14.5	Mathavan (1990)
<i>Palpopleura lucia</i> (Drury)	5	10		Hassan (1976)
<i>Pantala flavescens</i> (Fabricius)	6	12		Kumar (1984a)
<i>Pseudothemis zonata</i> (Burmeister)	several	13 ^{4,5}		Miyakawa (1969)
<i>Rhodothemis rufa</i> (Rambur)	1	10		Begum et al. (1990a)
<i>Sympetrum danae</i> (Sulzer)	several	11 ⁴		Waringer (1983)
<i>Sympetrum depressiusculum</i> (Selys)	many	10 ⁴		Katzur (1998)
<i>Sympetrum flaveolum</i> (Linnaeus)	?	12 ⁴		Taranova (1980)
<i>Sympetrum fonscolombii</i> (Selys)	many	11 ⁴		Katzur (1998)
<i>Sympetrum obtusum</i> (Hagen)	9	9, 10	9.1	Krull (1929)
<i>Sympetrum pedemontanum</i> (Müller in Allioni)	4	10 ⁴		Münchberg (1938)
<i>Sympetrum sanguineum</i> (Müller)	1	10		Gardner (1950)
<i>Sympetrum striolatum</i> (Charpentier)	38	10-12 ⁴	10.8	Bulimar (1969)
<i>Sympetrum vicinum</i> (Hagen)	4	12 ⁴		Nevin (1929)

Table 2. Continued.

Species ¹	<i>n</i> ²	No. stadia ³	Average	Reference
<i>Sympetrum vulgatum</i> (Linnaeus)	?	9 ⁴		Münchberg (1930a)
<i>Tauriphila risi</i> (Martin)	many	14 ^{4,5}		Rodrigues Capitulo (2000)
<i>Tramea virginia</i> (Rambur)	5	13		Kumar (1989)
<i>Trithemis annulata scoreceii</i> Nielsen	2	11		El Rayah & El Din Abu Shama (1978)
<i>Trithemis festiva</i> (Rambur)	1	12		Kumar (1972a)
<i>Urothemis assignata</i> (Selys)	6	10 ⁴		Forge (1981)
<i>Urothemis signata signata</i> (Rambur)	3	13		Begum et al. (1991)
<i>Zyxomma petiolatum</i> Rambur	10	12, 13	12.2	Chowdhury & Akhteruzzaman (1983)
ZYGOPTERA				
Calopterygidae				
<i>Calopteryx aequabilis</i> Say	27	13 ⁴		Martin (1939)
<i>Calopteryx haemorrhoidalis</i> (Vander Linden)	many	14 ⁴		Schütte & Weinheber (unpubl.)
<i>Calopteryx maculata</i> (Beauvois)	11	13 ⁴		Martin (1939)
<i>Calopteryx splendens splendens</i> (Harris)	many	13 ⁴		Schütte et al. (1999)
<i>Calopteryx virgo</i> (Linnaeus)	many	13 ⁴		Schütte et al. (1999)
Coenagrionidae				
<i>Argia moesta</i> (Hagen)	201	12-15	13.7	Legrís et al. (1987)
<i>Argia vivida</i> Selys	18	12-14	12.8	Leggott & Pritchard (1985)
<i>Cercion lindenii</i> (Selys)	several	14 ⁴		Thibault (1962)
<i>Cercion sieboldii</i> (Selys)	several	10, 11 ⁴	10.5	Naraoka (1987)
<i>Ceriagrion coromandelianum</i> (Fabricius)	3	12		Kumar (1980)
<i>Coenagrion caeruleum</i> (Fonscolombe)	34	11-14 ⁴	12.7	Conesa García (1990)
<i>Coenagrion hastulatum</i> (Charpentier)	1	10		Gardner (1954)
<i>Coenagrion mercuriale</i> (Charpentier)	1	13		Corbet (1955b)
<i>Coenagrion puella</i> (Linnaeus)	many	11 ⁵		Pickup & Thompson (1990)
<i>Coenagrion pulchellum</i> (Vander Linden)	14	11-14 ⁴	12.0	Balfour-Browne (1909)
<i>Enallagma boreale</i> Selys	7	11, 12 ⁴	11.4	Lebeuf & Pilon (1977)
<i>Enallagma cyathigerum</i> (Charpentier)	1	15 ⁴		Balfour-Browne (1909)
<i>Enallagma carunculatum</i> Morse	613	9-13	11.1	Masseau & Pilon (1982b)
<i>Enallagma ebrium</i> (Hagen)	64	11-13 ⁴	11.5	Fontaine & Pilon (1979)
<i>Enallagma hageni</i> (Walsh)	650	10-14 ⁴	11.9	Masseau & Pilon (1982a)
<i>Enallagma vernale</i> Gloyd	81	13-15 ⁴	13.5	Rivard & Pilon (1977)
<i>Erythromma najas</i> (Hansemann)	1	15 ⁴		Balfour-Browne (1909)
<i>Ischnura elegans</i> (Vander Linden)	many	11 ⁵		Pickup & Thompson (1990)
<i>Ischnura verticalis</i> (Say)	605	10-13 ⁴	10.8	Franchini et al. (1984: 31)
<i>Pseudagrion rubriceps</i> Selys	6	10		Kumar (1979)
<i>Pyrrhosoma nymphula</i> (Sulzer)	2	12, 13 ⁴	12.5	Balfour-Browne (1909)
<i>Xanthocnemis zealandica</i> (McLachlan)	several	13		Scott (1971)

Table 2. Continued.

Species ¹	<i>n</i> ²	No. stadia ³	Average	Reference
Lestidae				
<i>Lestes barbarus</i> (Fabricius)	15	11,12 ⁴	11.1	Loibl (1958)
<i>Lestes dryas</i> Kirby	1	11		Gardner (1952)
<i>Lestes eurinus</i> Say	25	13-15, 17	14.5	Pellerin & Pilon (1977)
<i>Lestes praemorsa</i> Selys	1	15		Kumar (1972b)
<i>Lestes sponsa</i> (Hansemann)	16	10-12 ⁴	11.3	Loibl (1958)
<i>Lestes viridis</i> (Vander Linden)	many	10		Prenn (1927)
<i>Sympecma fusca</i> (Vander Linden)	1	11 ⁴		Geijskes (1929)
<i>Sympecma paedisca</i> (Brauer)	?	10 ⁴		Prenn (1928)
Megapodagrionidae				
<i>Austroargiolestes isabellae</i> (Theischinger & O'Farrell)	2	8, 9 ⁴	8.5	Murray (1992)
Platycnemididae				
<i>Platycnemis pennipes</i> Pallas	several	11 ⁴		Thibault (1962)
Pseudolestidae				
<i>Rhipidolestes aculeata aculeata</i> Ris	several	14 ⁴		Tabaru (1975)

¹ Only one entry is given for each species. If more than one published account exists for the same species, the one chosen for inclusion is that involving the greatest number of larvae.

² Number of larvae completing development.

³ Number of stadia, including the prolarva as stadium 1.

⁴ Number of stadia raised by one from the published value so as to include the prolarva as stadium 1.

⁵ Number of stadia estimated by extrapolation.

⁶ Number of stadia obtained from rearing early stadia from the egg and estimating stadia from field samples.

Stadium

'Stadium' and 'instar' are not synonymous (Jones 1978). An instar begins at the moment of apolysis, and a stadium begins with ecdysis. Although the old Linnean definition of the instar, beginning with ecdysis, may still retain some convenience (Richards & Davies 1977: 363), the term stadium is already so widely used in its correct meaning (especially by French- and German-speaking odonatologists) that it no longer seems justified to postpone its adoption in English texts also.

Number of stadia

Compared with the Holometabola (Endopterygota), Heterometabola (Exopterygota) typically feature a larger and more variable number of stadia (Hinton & Mackerras 1970: 92). Ephemeroptera, as Palaeoptera and as the closest known relatives of Odonata, sometimes have as many as 45 stadia (Chapman 1971: 388). Tillyard (1917: 73) reported that the number of stadia of Odonata is not constant, either between or within species, and that it varies from 11 through 15 (including the prolarva). Information on this subject tends to come from discrete studies undertaken as opportunity offers without attempts being made to standardise rearing conditions (e.g. provision of food, temperature, photoperiod). Also, because mortality of larvae in culture is typically high in early stadia (see Rodrigues Capitulo 1980), most species records of the number of stadia are based on very few individuals. Since Tillyard's generalisation, there have been two attempts to review such records. Münchberg (1938) listed results for 24 species, several of which fell outside the range specified by Tillyard; and Corbet (1999: 208) summarised records for 85 species, giving notice that the source data would be published in due course. The present paper fulfils that undertaking.

The data available to me when preparing this paper are listed in Table 2, and in synoptic form in Table 3 and Figure 1. The extent of variation that can occur within a species, and sometimes even among siblings reared under identical conditions from the same batch of eggs, is shown in Table 4. From these data the following conclusions can be drawn: (1) the number of stadia varies within and between species; (2) the number of stadia of Odonata varies from 8 through 18 (Anisoptera: 8 through 18; Zygoptera: 8 through 17), the average being between 12.2 and 12.5 in both suborders; (3) no precise morphological or ontogenetic information is conveyed by specifying the ordinal number of a stadium, except perhaps for the first three and the last three stadia, because only these six stadia are likely to possess unvarying morphology (see Corbet 1951; Dunkle 1980; Masseur & Pilon 1982b; Leggott & Pritchard 1985); (4) there are indications that certain families of Anisoptera (Aeshnidae, Corduliidae and Gomphidae) have more stadia than Libellulidae and the families of Zygoptera ($\chi^2 = 19.365$ for 10 degrees of freedom, $0.05 > p < 0.02$); and (5) more than 90% of records from both suborders fall in the range 10 through 16 stadia. Indeed, to specify the ordinal number of an intermediate stadium implies a non-existent precision, because one cannot state confidently how many stadia there will be in any individual.

The most informative way of designating the developmental stage of larvae of intermediate size remains to give their linear dimension (preferably headwidth) or, for larger larvae, to use the F-x notation. Verschuren (1991) has proposed a scheme for designating successive stages in larval growth from this point of view, identifying a large, intermediate size class in which stadia cannot readily be assigned ordinal numbers. We note from Table 3 that families whose larvae exhibit rapid growth (see Krishnaraj & Pritchard 1995), namely Libellulidae, Coenagrionidae and Lestidae, feature fewer stadia. Omitted from this analysis and Table 2 is one strikingly anomalous report that assigns 20 and 24 stadia, respectively, to two species of trithemistine libellulid, *Trithemis arteriosa* (Burmeister) and *T. furva* Karsch (Osborne 1995). This result is so far removed from any previous finding that it exposes the possibility that these larvae

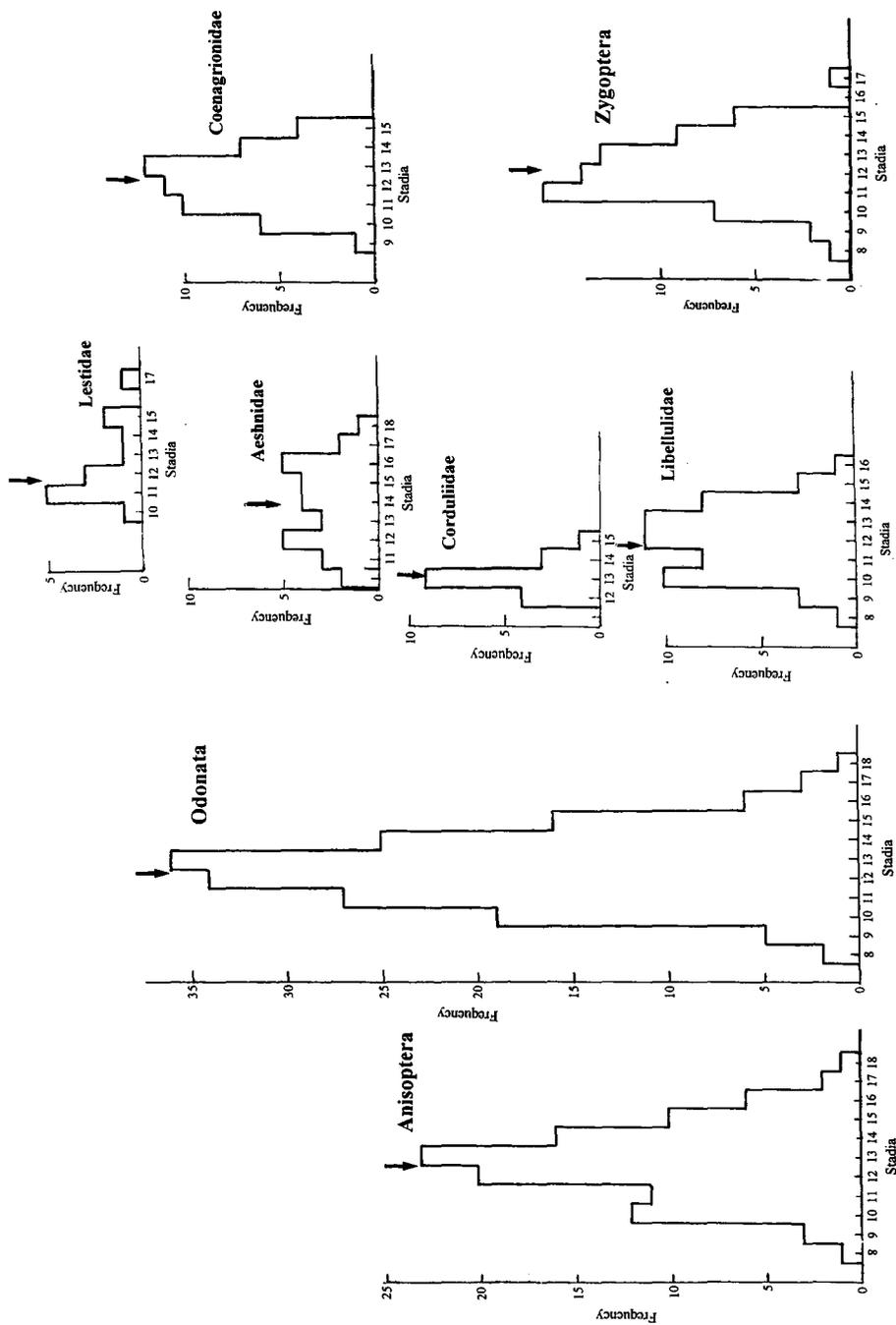


Figure 1. Frequency distributions of stadia required to complete larval development in different taxa of Odonata. Arrows indicate the position of mean values.

were experiencing hormonal perturbation and/or that the conditions under which they developed exposed them to some unusual stimulus that induced supernumerary ecdysis (see Schaller 1989: 108). Hormonal control of ecdysis is mediated through paramedian anterior neurosecretory A cells of the brain (Charlet & Schaller 1976). If either the pars intercerebralis of the brain or the prothoracic or ventral glands that produce the hormone ecdysone are destroyed, ecdysis is prevented and a 'permanent' larva' that lacks ecdysone is produced (Charlet & Schaller 1975).

The representation of species and families in Tables 2-4 is unavoidably weighted towards taxa that are relatively easy to rear in captivity. Needed now are data from other families in order to obtain a more balanced taxonomic representation. Despite detailed studies of larvae raised under uniform conditions (see references in Table 4), no sustainable hypotheses have emerged to explain the pattern of variation in the number of stadia within a species. Several of the authors cited in Table 4 have regarded this variation as a manifestation of "developmental types", implying a qualitative difference between the stadium categories (e.g. Rivard & Pilon 1977).

Table 3. Average number of stadia required to complete larval development in Odonata, by family.

Family	No. genera	No. species ¹	Average no. of stadia	Range	% of records in stadium range:	
					11-13	10-16
Anisoptera						
Aeshnidae	4	14	13.9	10-18	37.9	90.0
Corduliidae	4	12	13.2	12-15	76.5	100.0
Gomphidae	5	7	13.9	12-15	44.4	100.0
Libellulidae	22	44	11.6	8-16	53.6	92.9
All Anisoptera	37	80	12.5	8-18	50.9	93.9
Zygoptera						
Calopterygidae	1	5	13.2	12-13	80.0	100.0
Coenagrionidae	10	22	12.2	9-15	64.7	98.0
Lestidae	2	8	11.7	10-17	60.0	92.9
All Zygoptera	16	38	12.2	8-17	52.4	96.3
Total (both suborders)	53	118	12.4	8-18	51.5	94.4

¹ For scoring purposes, entries for subspecies are combined under the species concerned which accordingly comprises only one entry.

Table 4. Variation in number of larval stadia.

Species	n	Stadia ¹										Reference			
		9	10	11	12	13	14	15	16	17	18				
<i>Aeshna caerulea</i>	50						94	6							Sternberg (1990: 71)
<i>Aeshna cyanea</i> ²	28			4	32	57	7								Degrange & Seassau (1964)
<i>Aeshna cyanea</i> ²	170			6	81	11	2								Schaller (1960: 766)
<i>Aeshna juncea</i>	55									71	29				Sternberg (1990: 77)
<i>Aeshna mixta</i> ²	55		67	33											Schaller & Mouze (1970)
<i>Aeshna subarctica</i>	34								41	9	50				Sternberg (1990: 82)
<i>Anax junius</i> ³	29					17	83								Beesley (1972: 35)
<i>Anax junius</i> ⁴	33		3	18	76	3									Beesley (1972: 35)
<i>Argia moesta</i> ^{2,5}	80				8	50	40	3							Legris et al. (1987)
<i>Argia moesta</i> ^{2,6}	83				1	27	55	17							Legris et al. (1987)
<i>Enallagma</i>															
<i>carunculatum</i>	613	4	17	46	29	41									Masseau & Pilon (1982b)
<i>Enallagma ebrium</i>	64			42	47	11									Fontaine & Pilon (1979)
<i>Enallagma hageni</i> ⁷	650		1	25	57	17	1								Masseau & Pilon (1982a)
<i>Ischnura verticalis</i> ⁷	605		36	48	16	1									Franchini et al. (1984: 31)
<i>Lestes eurinus</i>	25					24	12	60	4						Pellerin & Pilon (1977)
<i>Libellula julia</i> ⁷	57					7	39	47	7						Desforges & Pilon (1989)
<i>Somatochlora alpestris</i>	118				54	34	12								Sternberg (1990: 59)
<i>Sympetrum striolatum</i> ²	38		21	76	3										Bulimar (1969)

¹ Numbers are given as percentages. Prolarva included as the first stadium. Included in the table are samples comprising 25 or more larvae, all of which were reared in captivity at the same time under similar conditions of temperature and photoperiod. Number of stadia raised by one from the published value so as to include the prolarva as stadium 1.

² Cohort from one oviposition by one female.

³ Larvae raised at 21°C.

⁴ Larvae raised at 31°C.

⁵ Larvae raised at 30°C.

⁶ Larvae raised at 32°C.

⁷ Larvae raised at 25°C and 16:8 photoperiod.

A correlation between the duration of embryogenesis and the subsequent number of stadia was detected in two species of *Aeshna* (being negative in *A. cyanea* and positive in *A. mixta*) and in *Enallagma ebrium* (positive) but no generalisation from these conflicting results has emerged. In other instances, however, external factors do indeed appear to affect the number of stadia. Field populations of *Cercion sieboldii*

(Naraoka 1987) and *Coenagrion hastulatum* (Johansson & Norling 1994) and, under experimental conditions, larvae of *Enallagma aspersum* (Hagen) and *E. hageni* exposed to unnatural conditions of temperature (elevated) and photoperiod (short) (Ingram 1975, 1976) may feature an additional ecdysis interpolated late in larval life; in the species of *Enallagma* this can happen in stadia F-2 and F-1 but not in F-0, leading to size increments in subsequent stadia (including F-0) and perhaps preventing emergence in late autumn (Ingram & Jenner 1976). Likewise, prolongation of F-1 by long photoperiods characteristic of midsummer causes larvae of *Pyrhosoma nymphula* to enter an extra stadium, recognisable as such by the size of the wing sheaths and the headwidth-to-wing-sheath ratio (Corbet et al. 1989). A similar response in F-1 *Coenagrion angulatum* Walker produces an outsize F-0 that usually cannot complete emergence, probably because of deformation of the wing sheaths (Sawchyn 1971). Supernumerary stadia have been detected also in field populations of *Asiagomphus pryleri* (Aoki 1994).

Temperature correlates positively with the number of stadia in *Coenagrion caerulescens* (Conesa García 1990), *Lestes eurinus* (Pellerin & Pilon 1977) and *Orthetrum sabina* (Mathavan 1990) and negatively in *Anax junius* (Beesley 1972; and see Kime 1974), *Argia vivida* (Leggott & Pritchard 1985b) and *Brachythemis contaminata* (Mathavan 1990). When larvae of *Ischnura verticalis* were reared at constant temperature and photoperiod, fewer stadia predominated in cohorts exposed as embryos to 9-10 or 13-14°C and more stadia predominated in cohorts exposed to 11-12°C (Franchini et al. 1984). Despite extensive research devoted to this matter, especially by Jean-Guy Pilon and co-workers (e.g. Masseur & Pilon 1982a; Franchini et al. 1984) no unifying hypothesis has emerged to rationalize variation in stadia number. This being so, it may be premature to refer to larvae exhibiting different stadia numbers as 'types', even though the rate of growth of some species (e.g. *Aeshna mixta*, Schaller & Mouze 1970 and probably *Cercion sieboldii*, Naraoka 1987), as expressed in size increase at successive ecdyses, differs according to eventual stadium number and is detectable from the outset. A different inference might be drawn from growth patterns of *Ischnura verticalis* when the data of Franchini et al. (1984) are reanalyzed (Corbet 1999: fig. 7.1). The pattern they form (Fig. 2) raises the possibility that the destiny of individuals having the most stadia (i.e. 12 and 13) is determined in about F-5 when the positive regression of stadium number and stadium duration abruptly changes sign so that stadium duration declines during F-4 to F-2, then to revert to the previous trend and increase during F-1 and F-0.

Some, perhaps most, species seem to possess a compensating mechanism whereby, regardless of the number of stadia, the size of F-0 varies little, as in *Aeshna cyanea* (DeGrange & Seasseau 1964), *Lestes eurinus* (Pellerin & Pilon 1989) and *Libellula julia* (Desforges & Pilon 1989). In *Anax junius*, when temperature correlates with the number of stadia, size at each of two temperatures differs markedly (for the same stadium) from stadium 5 onwards but hardly at all in F-0 (Beesley 1972). Likewise, the ratios for size increase at ecdysis (i.e. growth ratios) for *Epithea cynosura* may vary seasonally among different larval cohorts, but uniformity of size is achieved in F-0 because smaller F-1 larvae increase more in size at ecdysis (Johnson 1987). On the other hand, some species show a clear correlation between eventual size and the number of stadia, this

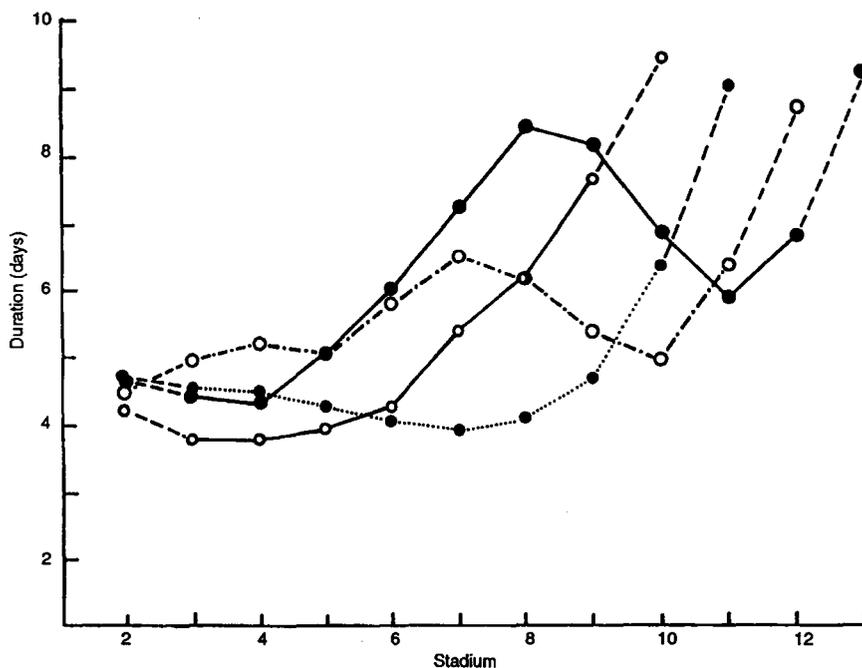


Figure 2. Durations of successive larval stadia of *Ischnura verticalis* larvae in four categories, namely those completing direct development in 10, 11, 12 and 13 stadia, respectively. Values for stadia 2 and F-0 are averages; averages for all other stadia were smoothed by a moving average of 3. Larvae were reared at 25°C and LD 16:8 from eggs laid by wild-caught females at 46°N in Quebec, Canada. Trends of increasing or decreasing duration change direction abruptly twice in developmental categories 12 and 13. Data recalculated from Franchini et al. 1984. (From Corbet 1999).

correlation being positive for *Argia moesta* (Legris et al. 1987), *A. vivida* (Leggott & Pritchard 1985) and *Enallagma hageni* (Ingram & Jenner 1976) but negative for *Aeshna mixta* (Schaller & Mouze 1970), *Brachythemis contaminata* and *Orthetrum sabina* (Mathavan 1990).

Duration of stadia

Duration of successive stadia does not always increase by smooth progression, as would be expected from the increase in body mass at each ecdysis. Examples of stadium-duration profiles (Fig. 3) allow three conclusions: (1) some species do indeed show a smooth and steady increase in duration; (2) sometimes the progression can be reversed in intermediate stadia (Fig. 2); and (3) there can be a disproportionately great increase in the duration of F-0. It is noteworthy that in early stadia of some species (e.g. *Orthetrum sabina* at 37°C, Fig. 3F) several stadia may last only 2 or 3 days; and

the raw (unsmoothed) data for *Pseudagrion rubriceps* (Fig. 3C) show that this species completed stadium 4 in only 1 day. Indeed the possible range of duration of stadia (excluding the prolarva) of Odonata extends from 1 day to more than 1 year (Corbet 1984, unpublished observations on *Somatochlora arctica*). The species providing data for Figure 3 are all tropical-centred species that characteristically exhibit unregulated development (i.e. lack larval diapause) deriving from populations just beyond the northern limit of the Tropics, where there is a wide seasonal swing in temperature and photoperiod. All were reared in captivity under permissive ambient temperature showing diel and seasonal fluctuation except for *Orthetrum sabina* (Fig. 3F), reared under $37 \pm 1^\circ\text{C}$ and *Diplacodes trivialis* (Fig. 3B) in stadia F-3 to F-0 which were exposed to significantly lower (i.e. winter) temperatures and photoperiods. It is noteworthy that in Figure 3E stadium duration rises steeply in F-1 and F-0, perhaps reflecting an incipient mechanism for seasonal regulation by arresting growth during the cold season. In *Aeshna cyanea* stadium duration declines steadily during stadia 1-5 and increases thereafter (Schaller 1960: 774) whereas in *A. mixta* stadium duration increases smoothly and rapidly throughout larval development (Schaller & Mouze 1970). Two late-stadium larvae of *Aeshna grandis* (Linnaeus) which suspended development at a time of year when rapid growth would have been expected, were found to be harbouring cercariae of

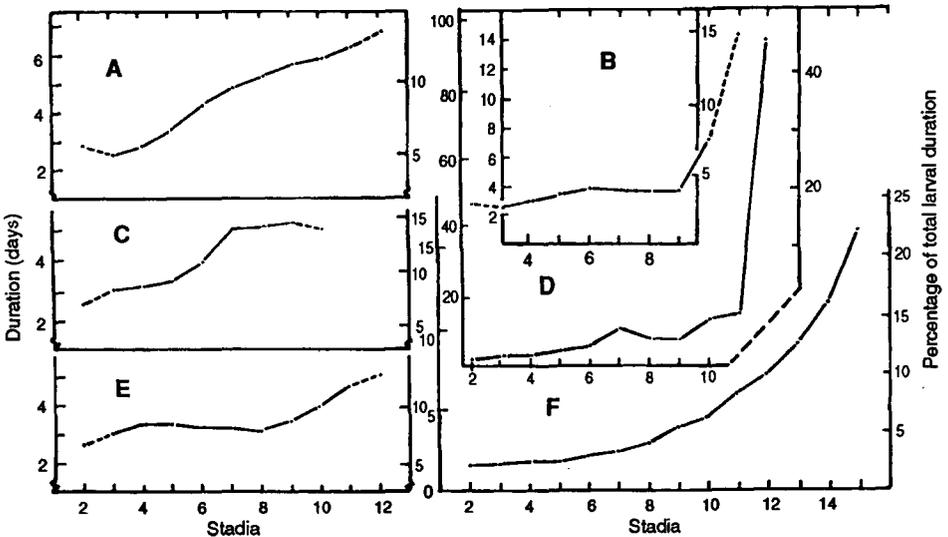


Figure 3. Durations of successive stadia in tropical-centred Odonata exhibiting direct development. Values on left ordinates are stadium averages, unsmoothed for stadia 2 and F-0 and for all stadia in D, and smoothed by a moving average of 3 for other stadia in A-C, E and F. Values on right ordinates are stadium durations as percentages of total larval duration. Data derive from studies listed in Table 2, unless specified - (A) *Pantala flavescens*; (B) *Diplacodes trivialis* (from Kumar 1984b); (C) *Pseudagrion rubriceps*; (D) *Neurothemis tullia tullia* (from Kumar 1988); (E) *Ceriagrion coromandelianum*; (F) *Orthetrum sabina*, reared at 37°C . (From Corbet 1999).

a parasite (U. Norling pers. comm. 2001). Much remains to be learnt about factors controlling stadium duration.

Growth ratios

Calvert (1929: 256-257) appears to have been the first to analyse growth ratios (GR) in Odonata, noting that the GR often exceeds the value of 1.26 expected from the predictions of Dyar and Przibam for hemimetabolous insects (Przibam & Megusar 1912). Schaller (1960: 767) showed that GR in *Aeshna cyanea* correlated negatively with the number of stadia, thus allowing F-0 larvae to be of uniform size, regardless of the number of stadia. Schaller also showed (1960: 768) that ontogenetic profiles for GR for a given dimension in *A. cyanea* were far from smooth, and differed widely depending on the number of stadia, a finding confirmed by Degrange & Seasseau (1964: 101). This puzzling phenomenon was investigated in greater depth by Jean-Guy Pilon and co-workers. The resulting array of ontogenetic profiles (Fig. 4) shows that (1) profiles for different dimensions can differ widely within and between species; (2) for certain dimensions (e.g. headwidth, metathoracic femur length and prementum length in *Argia moesta*) GR follows a smooth, declining progression during ontogeny, whereas for others (e.g. the same dimensions in *Libellula julia*) successive values of GR may fluctuate violently and irregularly; (3) profiles for the same dimension are broadly similar regardless of the number of stadia; (4) certain dimensions (e.g. length of wing sheaths in all species) exhibit *allometric* growth, characterised by very high values of GR confined to later stadia; and (5) regardless of the number of stadia, there is a characteristic GR profile for each dimension. It is noteworthy that, except for wing sheaths, all dimensions portrayed in Figure 4, despite the irregularities revealed by analysis, have conventionally been deemed to exhibit *isometric* growth; and that dimensions showing a smooth progression of GR (see [2] above) will, for this reason, be preferred as a measure of stage of larval development; thus headwidth and metathoracic femur length emerge as the dimensions of choice for this purpose. The values of GR shown in Figure 4, excluding those for wing sheaths, produce median values for the three species as shown in Figure 5. The medians for structures growing isometrically lie well below 1.26 (Przibam's notional value for Hemimetabola), whereas the medians for the wing sheaths, which grow allometrically, predictably lie well above 1.26.

That aeshnid larvae tend to have more stadia and to develop more slowly than libellulid larvae might lead one to expect that growth ratios of Aeshnidae would be lower, on average, than those of Libellulidae. This indeed appears to be so (Fig. 6), the GR averaging 1.232 in Aeshnidae and 1.301 in Libellulidae. Likewise one might expect growth ratios within a species to be lower in larvae that have more stadia. The data provided by Sternberg (1990) are eminently suited for testing this expectation. As it happens, these data reveal only a very slight tendency in this direction in three species of *Aeshna*, namely *A. caerulea* (p. 70), *A. juncea* (p. 76) and *A. subarctica elisabethae* (p. 81), but not in *Somatochlora alpestris* (p. 58). For example, means of GR for larvae of *A. subarctica elisabethae* with 16, 17 and 18 stadia, respectively, are 1.18, 1.17 and 1.16. One can only say that, if such a correlation exists within species, it is not pronounced.

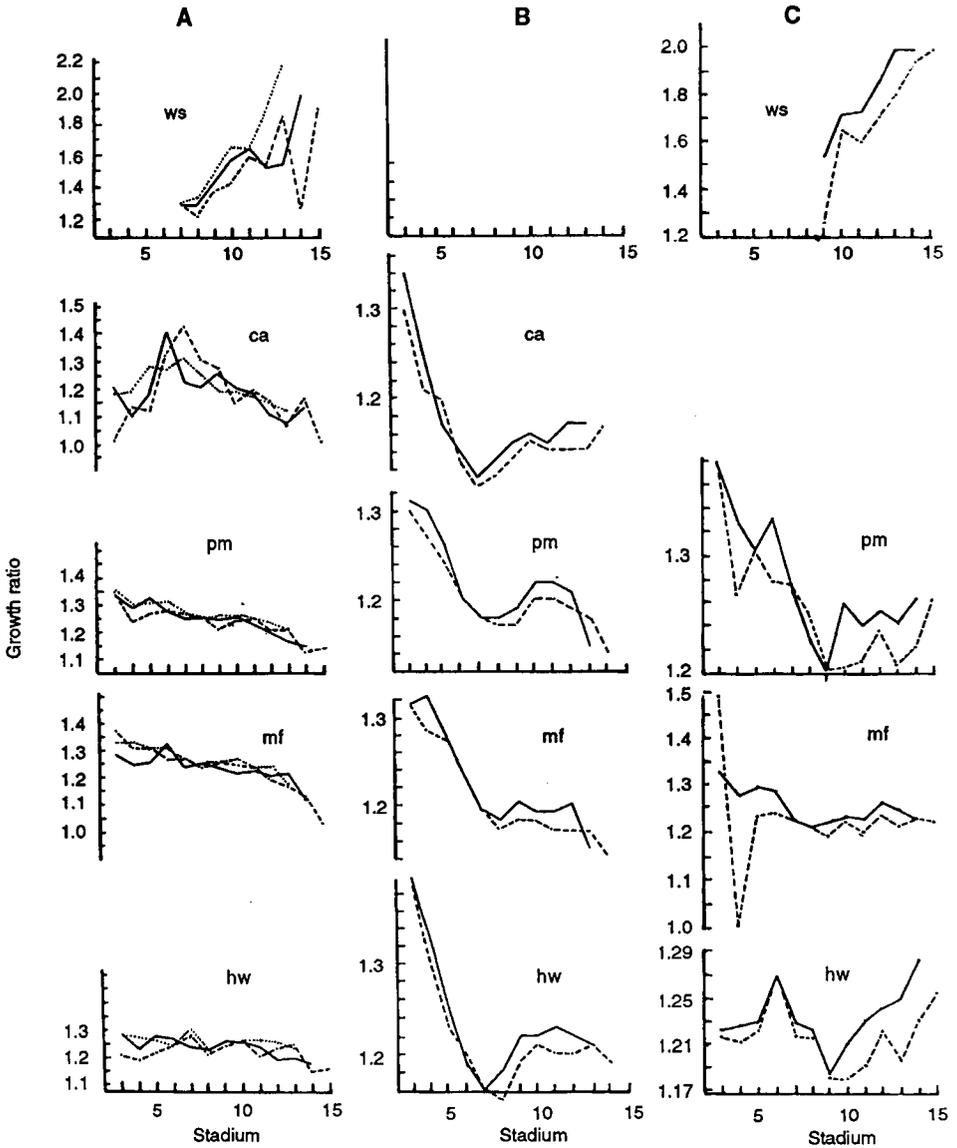


Figure 4. Ontogenetic profiles for growth ratios for different dimensions according to the number of stadia needed to complete larval development in three species of Odonata – (A) *Argia moesta*, exposed to 25°C and LD 16:8; (B) *Enallagma vernale*, 25°C and LD 14:10; and (C) *Libellula julia*, 25°C and LD 16:8. The growth ratio recorded refers to the ecdysis at which each stadium on the abscissa is entered. Symbols for each category of stadium number can be identified by tracing the position of the final stadium on the abscissa. Abbreviations for dimensions measured – ca: length of caudal appendage; hw: headwidth; mf: length of metathoracic femur; pm: length of prementum; ws: length of metathoracic wing sheath. (A) after Legris et al. (1987); (B) after Rivard & Pilon (1978); and (C) after Desforges & Pilon 1989. (From Corbet 1999).

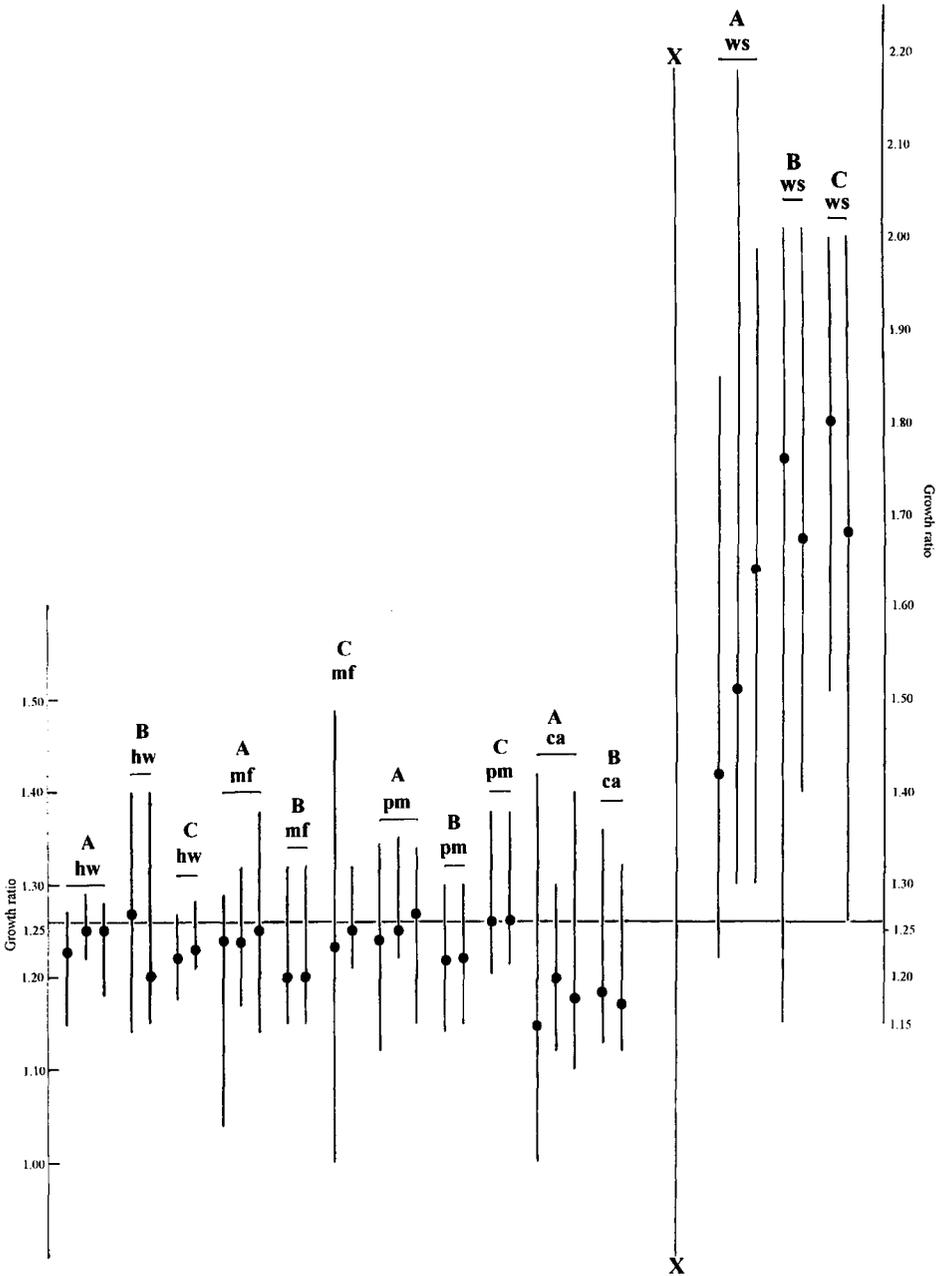


Figure 5. Ranges (vertical lines) and medians (filled circles) of growth ratios for different dimensions derived from data in Figure 4. The contrast between structures growing isometrically (left of vertical line, X-X) and allometrically (wing sheaths, right of vertical line) is noteworthy. The horizontal line marks the growth ratio considered by Przibam to be typical of Hemimetabola, namely 1.26. Abbreviations for species and dimensions as in Figure 4.

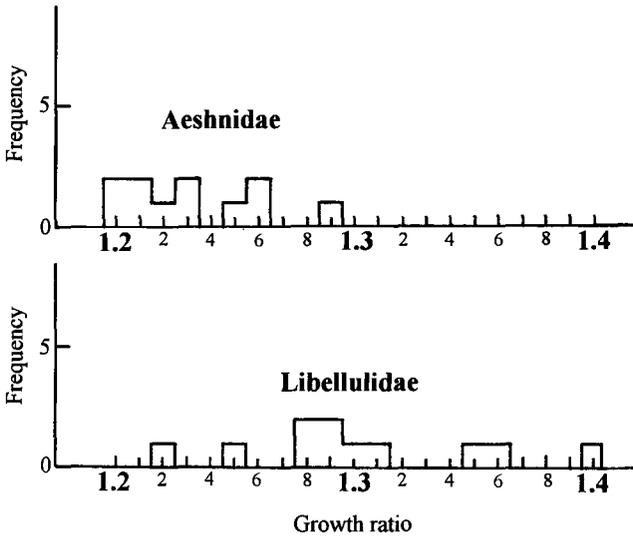


Figure 6. Frequency distributions of average growth ratios of headwidth for species of Aeshnidae and Libellulidae ($n = 11$ in both cases).

Values recorded in Figure 4 were derived from larvae reared under constant temperature and photoperiod, as specified in the figure legend. So they provide no information about possible short-term effects of external factors. We may note, however, that, apart from the constraining effects of diapause (probably unrepresented in Figs 3 and 4 which portray tropical-centred species), profiles are likely to vary according to the foraging and growth strategies of each species. Since the pioneer observations of Hodgkin & Watson (1958), it has been recognised that obligate pool dwellers, unlike riverine species, exhibit a rapid increase in growth rate as ambient temperature rises. Thus *Lestes sponsa*, an active pool dweller with a high temperature coefficient for growth, and to a lesser extent *Coenagrion puella* and *Ischnura elegans*, respond to elevated temperature at the same level of food provision by developing faster at the cost of reduced GR (Pickup & Thompson 1990). These two effects of elevated temperature provide the basis for inferring the existence of bivoltinism in unregulated odonates at low temperate latitudes when larvae and adults of the summer generation (which have developed at higher temperature) are smaller than those of the overwintering generation (Corbet 1999: 632). A dichotomy among larval Odonata with regard to the relationship between temperature and growth rate has been rigorously quantified by Krishnaraj & Pritchard (1995) and Pritchard et al. (2000) in their comparison between *Lestes disjunctus* Selys (which, like *L. sponsa*, develops rapidly and at high temperature in small ponds) and three species of Coenagrionidae. This elegant work points the way for similar ontogenetic studies on species of Odonata from a variety of microhabitats and with contrasting life styles. To compare profiles of percentage growth rate for a partivoltine clasper such as *Epiophlebia superstes* with those of an active sprawler

like *Pantala flavescens* would be highly informative. Indeed to determine such profiles for the main categories of larvae based on life style, morphology and microhabitat occupancy (see Corbet 1999: tables 5.6, 5.7) will be of great heuristic value.

Morphological change

The external morphology of odonate larvae is relatively well known for F-0 and, to a much lesser extent, for stadium 2 (e.g. Dunkle 1980; references by Pilon and co-workers cited in Table 4). For some species, including many listed in Table 2, the morphology has been described for all stadia. During the last three decades, a series of very detailed morphological descriptions of all stadia of several species of coenagrionids has come from Jean-Guy Pilon and co-workers at the University of Montreal (see references in Table 4). For two species of Anisoptera analytical descriptions are available of the ontogeny of certain structures (e.g. labium by Corbet 1951; antennae by Verschuren 1991).

Despite such detailed studies, little has been achieved towards translating the results into schemes for determining early-stadium larvae – an urgent need for the successful prosecution of balanced studies of larval ecology.

Indeed, unless other approaches to the identification of early stadia (e.g. DNA analysis, Hadrys et al. 1992; and see Zloty et al. 1993) become readily available, the discovery of determination criteria for early stadia is probably one of the most useful contributions investigators could make to our understanding of the natural history of the odonate larval stage. This will not be easy: attempts by Masseur & Pilon (1982b) to discover characters by which all stadia of four species of *Enallagma* can be distinguished failed to find means of distinguishing *E. ebrium* from *E. hageni* and *E. boreale* from *E. vernale* in stadia 2-4.

Conclusion

In this review I have proposed a terminology for structures and events in larval development of Odonata that will achieve conformity with terms used in other insect orders in the light of accepted views of homology in insects. All terms proposed have secure precedent for use within and beyond the Odonata. Analysis of records available for the number of stadia required to complete larval development reveals that the range for Odonata differs very little between the two suborders (Anisoptera: 80 species, 8-18 stadia; Zygoptera: 38 species, 8-17 stadia), averaging 12.5 and 12.2 stadia respectively. The number of stadia varies between and within species, and sometimes among individuals emanating from a single egg batch: yet no unifying hypothesis exists to rationalize this variation, and no evidence exists to support the view that conspecific larvae featuring different numbers of stadia constitute 'types', a term that implies discontinuous and qualitative, rather than continuous, variation among such larvae. This finding supports the contention that it is inappropriate, indeed misleading, to use ordinal stadium number (except for the first three and the last three stadia) to specify a stage in

ontogeny, which is much better done by citing a body dimension that exhibits a smooth and isometric growth-ratio profile, such as headwidth or mid-femur length. Analysis of growth ratios throughout ontogeny shows these to form a smooth progression for some structures and some species, but not for others, in which profiles fluctuate irregularly during development. The most promising avenues for future research in this field of enquiry include investigation of prospective correlations between larval life style on the one hand and the total number of stadia and growth-ratio profiles on the other. A long-standing, and as yet unsatisfied, need to advance our understanding of larval ecology is the discovery of means for identifying larvae to species in early stadia.

Acknowledgements

It is a pleasure to thank Steve Brooks, Gianmaria Carchini, Reinhard Jödicke, Andreas Martens, Ulf Norling, Michael Samways, Frank Suhling and Hansruedi Wildermuth for supplying information. Ulf Norling kindly reviewed the manuscript in draft.

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