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**FIELD NOTES ON EMERGENCE OF
PANTALA FLAVESCENS (FABRICIUS)
IN CENTRAL INDIA
(ANISOPTERA: LIBELLULIDAE)**

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A total of 611 exuviae were collected within a period of 45 days during April-May, 2004 from the walls of an open cement drain at Nagpur, India. The daily record of this collection revealed that 50% of the total emergence was completed by the 14th day and the sex ratio is considerably in favour of ♂♂ (1.4:1). The ♀♀ emerge earlier (protogyny) and the ME₅₀ for ♀ and ♂ was observed on the 10th and 18th day, respectively. Protogyny probably provides adequate time for the ♀ to develop her ovaries. 194 exuviae (31.75%) were collected from the north wall, which was completely in shade, and 417 (68.25%) from the south wall, which receives sunlight throughout the day. On the north wall, 44.7% exuviae were collected at a height of 30-45 cm from the water level, while from the south wall, 57.2% exuviae were collected at a height up to 15 cm and 28.4% between 15-30 cm. The present findings indicate that sunlight and temperature not only determine the choice of direction of the emerging larva but also initiate an early commencement of Stage I of metamorphosis (shortening the time between the surfacing of the larva and splitting its thoracic cuticle), which results in the shorter distance climbed by the larvae on the south wall for the final moult.

INTRODUCTION

The emergence of insects is an important phenological event because the timing of insect mating is critical for population maintenance. One of the best methods to monitor odonate populations, particularly Anisoptera, is the collection and documentation of the exuviae (MOORE & CORBET, 1990; CORBET, 1999). Examination of odonate exuviae at emergence allows various parameters (sex ratio, mean body weight, number, seasonal pattern) to be investigated before any bias by dispersal or differential adult mortality appears (MICHIELS & DHONDT, 1989; AOKI, 1999; PURSE & THOMPSON, 2003). Thus FOSTER & SOLUK

(2004) undertook an exuviae count to predict larval densities and life history information of the endangered dragonfly *Somatochlora hineana*, DOI (2008) reported a corresponding delay in emergence of *Orthetrum albistylum speciosum* with global warming and RICHTER et al. (2008) proposed a model for predicting the emergence of dragonflies in a changing climate by observing the emergence of *Gomphus vulgatissimus* in the laboratory under controlled environmental conditions.

As soon as the monsoon arrives in the Indian subcontinent, numerous *Pantala flavescens* are found egg-laying vigorously in temporary ponds, puddles, water accumulated on tar-roads, play grounds, rice fields and even on terraces of cement buildings (KUMAR, 1984). KUMAR (1976) studied the life history of *P. flavescens* and reported that the larval development is completed in 50-60 days. Although this species is found in large numbers all over the Indian subcontinent, no major efforts have been undertaken to study their emergence pattern, so much so, that during the plenary session on “*Seasonal ecology of Pantala flavescens in the Indian subcontinent*” organized at the 9th International Symposium of Odonatology at Madurai, India, CORBET (1988) stated that “... Is that not a remarkable thing? This [*P. flavescens*] is an extremely common widespread species and yet it appears that very little is known about its emergence and maiden flight (in the Indian subcontinent)...”.

Last year, we published reports on the process of moulting (ANDREW & PATANKAR, 2010) and mortality during emergence (ANDREW, 2010) in *P. flavescens*. The present report describes the emergence pattern of *P. flavescens* during the pre-monsoon period in central India.

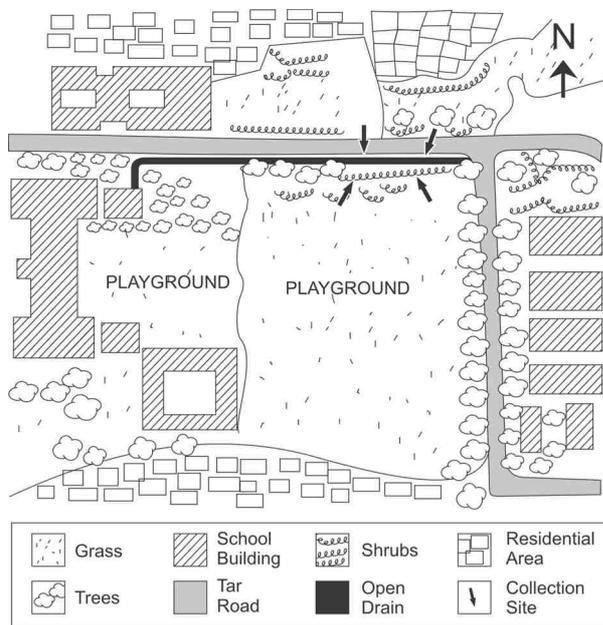


Fig.1. Map of the locality, indicating landscape elements and the study site.

MATERIAL AND METHODS

The city of Nagpur (21°10'N and 79°12'E) lies at the southern fringe of the Satpuda mountain ranges in central India. It is located on an undulating plateau

with altitude ranging between 274-305 m above mean sea level. During the study period, the minimum and maximum temperature was 20°C and 43°C, and the minimum and maximum humidity was 8% and 89%, respectively.

SITE. – The study site was a long, open cement drain running in a west–east direction located in the playing field of St. Johns School in Nagpur city (Fig.1). This drain was constructed just two months before the start of this study. It is 85 cm wide and 80 cm deep. Although this drain is little used and water moves very slowly, a water column of 10 inches accumulates at the bottom due to the presence of a single brick layer placed across its floor at regular intervals. The few grasses and weeds emerging along the brick layer were manually removed so that the larvae could use only the cement wall of the drain as an emergence support. An algal mat covered part of the water surface. During the study period, the south wall of the drain was always sunlit while the north wall of the drain was mostly in shade (Figs 2-3).

From 1st April till the cessation of emergence (15th May 2004), larval exuviae were collected from the site between 5.30 am and 7.30 am. The distance between the exuviae and water level was recorded for the first 20 days of observation. All the exuviae were brought to the laboratory and sexed. Dead and dying pharate adults were also collected and the reason for mortality during emergence was noted (ANDREW, 2010).

STATISTICAL ANALYSIS. – The Chi-square test was used to test the height climbed for emergence assuming that there was no association between height and the day of emergence.

OBSERVATIONS

A total of 611 exuviae, comprising of 319 males and 292 females were collected between 1st April and 15th May 2004. The daily collection of exuviae from the north and south wall of the drain is illustrated in Figure 4. A total of 194 exuviae (31.75%) were collected from the north wall and 417 (68.25%) from the south wall. The sex ratio was found to be 1.4:1 in favour of males ($p < 0.005$). Figure 5 illustrates the daily emergence of male and female during the study period. Fifty percent of the total emergence was observed by the 14th day and the females emerged earlier than the males. The EM_{50} for female and male was observed on the 10th and 18th day, respectively (Fig. 6). Statistical analysis (chi-square test) confirms that there was a direct correlation between the sex and the day of emergence



Figs 2-3. The open drain as seen from the eastern end, showing the accumulated water due to the presence of single brick layer placed across its floor at regular intervals: (2) the north wall in shade; – (3) the well-lit south wall of the drain.

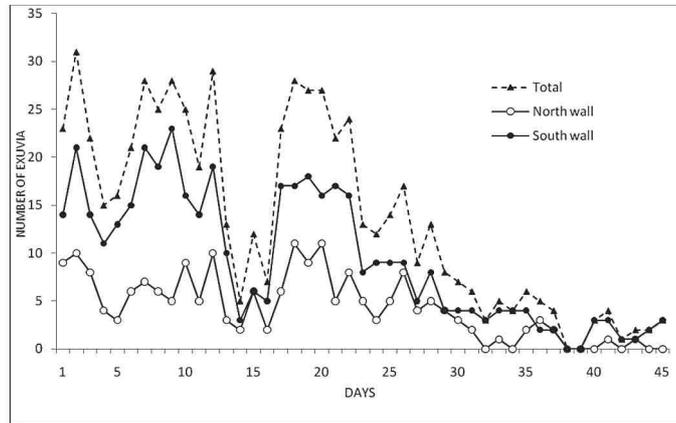


Fig. 4. Daily collection of *P. flavescens* exuviae from the north and south walls of the open drain.

and of the larva and with maximum emergence of females occurring between 2 and 12 days and that of males between 17 and 26 days.

The distance between the water level and the exuviae collected from the north and south walls in the first 20 days of observation is given in Figures 7 and 8, respectively. On the north wall, 44.7% exuviae were collected at a height between 30-45 cm, 23.5% above 45 cm, while 21% and 10.6% were collected from a height between 15-30 cm and 1-15 cm, respectively. Maximum emergence occurred at a height of 30-45 cm and minimum below 15 cm. Emergence occurred more or less equally on all days between 15-45 cm. Emergence took place preferably between 30-45 cm till the eighth day; later, there was a tendency towards an increase in the height for emergence.

On the south wall, 57.2% exuviae were collected at a height between 1-15 cm, 28.4% between 15-30 cm, while 10.6% and 3.8 % were collected from a height between 30-45 cm and above 45 cm, respectively. Chi square analysis confirms that maximum emergence occurred upto 15 cm with significantly fewer above 30

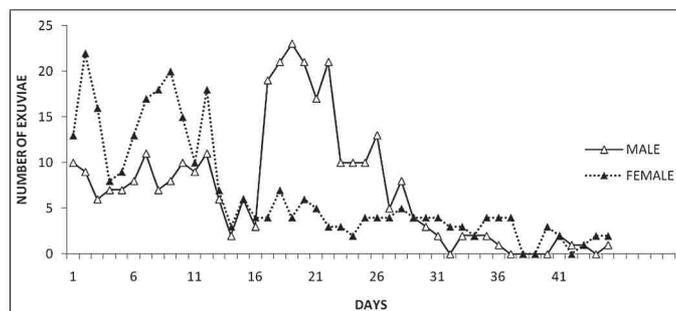


Fig. 5. Daily collection of *P. flavescens* male and female exuviae from the open drain.

cm. Below 15 cm, emergence occurred more or less with the same frequency but in the initial days it occurred preferably at a height of 6-15 cm. Below 6 cm was always preferred for emergence, whereas it occurred above 30 cm very rarely.

DISCUSSION

In dragonflies, two general types of emergence pattern caused by differences in seasonal regulation have been described. 'Spring species' emerge early in the year, have a tight seasonal synchrony with a short main emergence period of less than 4 weeks and undergo winter diapause in the final larval stage. In "summer species" emergence starts later in the year, is less synchronized and continues over several months (CORBET,1999). Emergence of *P. flavescens* before the onset of the monsoon in central India can be included in the "spring species" category but without the state of diapause in the final larval stage because this emergence was recorded in a newly constructed drain (2 months old at the start of this study) which clearly deletes the chances of the final instar larval stage undergoing diapause. Furthermore, in the Indian subcontinent, *P. flavescens* completes its life-cycle within 50-60 days (KUMAR, 1984). POYYAMOLI & PANDIAN (1985) reported the emergence of *P. flavescens* between 05:00 and 07:00 h which is probably the observation of the maiden flight rather than emergence since emergence in *P. flavescens* occurs between 21:00 and 24:00 h (ANDREW & PATANKAR, 2010).

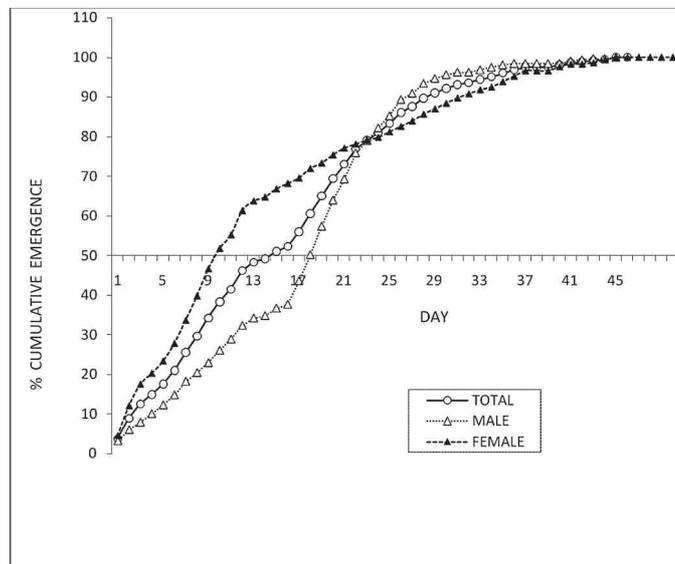
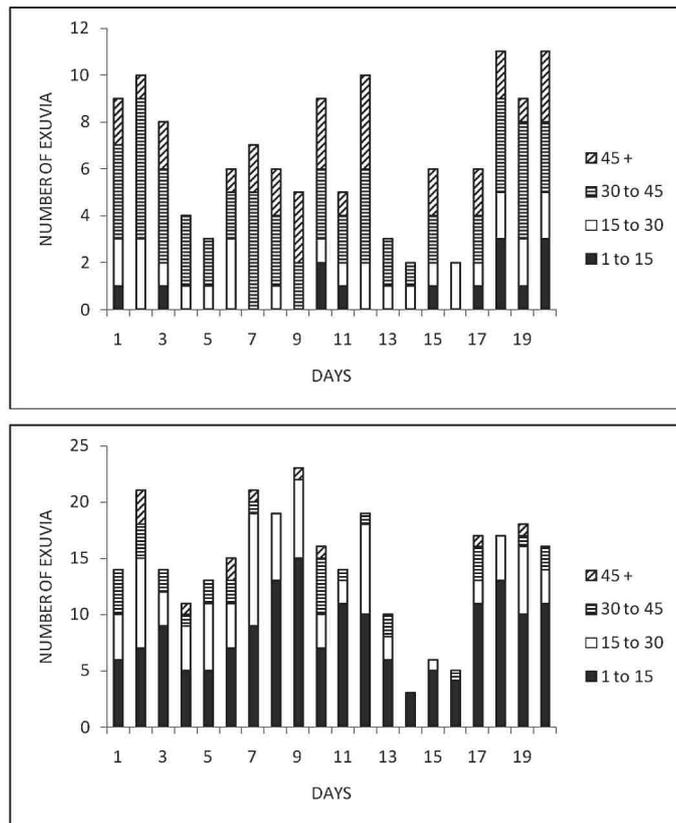


Fig. 6. Cumulative emergence of *P. flavescens* during the present study.

The sex ratio of Odonata at emergence should be in the ratio of 1:1 because of the sex determining mechanism which is of the XO-XX type (KIAUTA, 1969). But CORBET & HOESS (1998) observed that, in most of the cases during emergence, zygopteran males usually outnumbered females [but see WAAGE (1980) and BENNETT & MILL (1993)], the reverse being true for Anisoptera. Biased sex ratio during emergence is not uncommon in dragonflies (PURSE & THOMPSON, 2003) and recently DOLNY et al. (2010) reported female bias emergence in three species of *Gomphus* at four sites on the Morava river, Czech Republic. Although the origin of the imbalances remains unknown, the ratio of imbalance recorded in some odonates can be attributed to differential mortality of eggs and/or larvae, size selection predation of larger female larvae and differences in responses of male and female larvae to environmental factors, especially in later stadia (TROTTIER, 1966, 1973; DUNKLE, 1985; BAKER et al., 1992;



Figs 7-8. Collection of *P. flavescens* exuviae from different heights: (7) on the north wall of the drain; – (8) on the south wall of the drain.

CORBET, 1999). According to CROWLEY & JOHANSSON (2002), the sex ratio should be more male-biased in non-territorial dragonflies. *P. flavescens* is not a territorial dragonfly and a total male biased ratio was observed in the present study.

INDEN-LOHMAR (1997) observed that protandry, i.e. emergence of males before females, might result in strong positive selection in *Aeshna cyanea*. Males that emerge early enjoy increased copulation success. Late emergence among females, if spending a longer time in the F-O larval stage, may result in larger females which are therefore more fecund and enjoy a greater lifetime reproductive success. Thus protandry might sometimes result from selection acting on both sexes but in different directions. BISWAS et al. (1994) presumed that early emergence of males assures their presence when females return to the water for mating. In contrast, BANKS & THOMPSON (1985) found that, in *Coenagrion puella*, the females emerge significantly earlier than the males (protogyny) and postulated that an important parameter of early adult life is the time at which the adults are first present at a breeding site in breeding condition and that the significantly shorter immature period of males more than compensates for their late emergence in this species. In *P. flavescens* too, it is found that the females emerge before the males and the probable reason could be the one proposed by BANKS & THOMPSON (1985) for *C. puella*. In freshly emerged males of Anisoptera, the testicular follicles have already a large number of completely developed spermatozoa (ANDREW & TEMBHARE, 1993), whereas the females have immature ovaries in the pre-vitellogenic stage and need more time and nutrition for the development and maturation (vitellogenesis, choriogenesis) of their eggs (ANDREW & TEMBHARE, 1997). Thus, if the males emerge early, there are probably very few mature females available for the males during the pre-monsoon season. Thus protogyny like protandry might sometimes result from selection acting on both sexes but in different directions.

The usual height climbed by Zygoptera varies between 5-10 cm (CORDERO, 1995), for gomphids, it is 25-50 cm (KURATA, 1971; INOUE, 1979) and the typical modal height reached by libellulid species varies between 0-20 cm (CORBET, 1999). BISWAS et al. (1994) reported that the height climbed by five libellulid species, under laboratory conditions, were: *Brachythemis contaminata* 25.4-27.94 cm, *Tholymis tillarga* 9.14-19.81 cm, *Crocothemis s. servilia* 4.31-17.52 cm, *Diplocodes trivialis* 11.43-15.74 cm and *Orthetrum p. pruinosum* 8.38-12.95 cm. Various anomalies have been recorded regarding the distance climbed by the emerging larva, since the height climbed and speed of climbing are under the influence of various factors such as air and water temperature, humidity, body size and varies of the weather (TROTIER, 1966, 1973; CORDERO, 1995). WORTHEN (2010) found that the larvae of *Epiteca spinosa* climbed to mean height of 3.3 metres, an adaptation to flooding which is common during the emergence period, and the larvae preferred trees with corky bark instead of a peeling flaking trunk.

In *P. flavescens* it is difficult to standardize the height climbed by the larva since it shows a great variation from 1 to more than 45 cm.

In *Cordulia aenea amurensis*, the density of exuviae was directly influenced by the degree of sunlight, width of bog mat and depth of marginal zone in a small pond in Japan (UBUKATA, 1984). PURSE & THOMPSON (2003) found a positive correlation between emergence and duration of sunlight during the previous day while LUTZ (1968) found a positive relationship between emergence and sunlight and UBUKATA (1973, 1981) reported faster emergence at higher temperatures. PAULSON (1966) observed that larvae of pond-dwelling Anisoptera commonly congregate in the warmest microhabitats as metamorphosis proceeds. In a study in the UK, most of the larvae of *Leucorrhinia dubia* emerged on the northwestern margin where they would be warmed by the direct rays of the early morning sun (BEYNON, 1995). In the present study, 68.25% larvae of *P. flavescens* preferred the south wall, which received maximum sunlight, for emergence and the majority (57.2%) climbed to a height of between 1-15 cm, while just 10% of the larvae reached a height above 45 cm. Only 32.75% of larvae preferred the north wall, which did not receive sunlight even during high noon, and most of the larvae reached a greater height than those on the south wall (44.8% climbed up to 30-45 cm and 23.5% larvae were found above 45 cm on the north wall). This clearly indicates that, in a tropical region too, temperature and sunlight not only determine the choice of direction of the emerging larva, as observed in *Cordulia aenea amurensis* (UBUKATA, 1984) and other odonates (CORBET, 1999), but also initiate an early commencement of Stage I (shortening the time gap between coming out of water and the splitting of the thoracic cuticle) of the emerging dragonfly (ANDREW & PATANKAR, 2010), which in turn results in a shorter distance of height climbed by the larva for the final moult.

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REFERENCES

- ANDREW, R.J., 2010. Mortality during emergence of *Pantala flavescens* Fabricius (Anisoptera: Libellulidae) in central India. *Odonatologica* 39: 57-62.
- ANDREW, R.J. & N. PATANKAR, 2010. The process of moulting during final emergence of the dragonfly *Pantala flavescens* Fabricius. *Odonatologica* 39: 141-148.
- ANDREW, R.J. & D.B. TEMBHARE, 1993. Structure and development of the internal male reproductive organs in the dragonfly, *Tramea virginia* (Rambur) (Odonata: Anisoptera). *Funct. Develop. Morphol.* 3: 121-127.
- ANDREW, R.J. & D.B. TEMBHARE, 1997. The development and structure of the ovaries in the dragonfly, *Tramea virginia* (Rambur). *J. Adv. Zool.* 18: 86-95.
- AOKI, T., 1999. Larval development, emergence and seasonal regulation in *Asiagomphus pryleri*

- (Selys) (Odonata: Gomphidae). *Hydrobiologia* 394: 179-192.
- BAKER, R.L., M.R.L. FORBES, & H.C. PROCTOR, 1992. Sexual differences in development and behaviour of larval *Ischnura verticalis* (Odonata: Coenagrionidae). *Can. J. Zool.* 70: 1161-1165.
- BANKS, M.J. & D.J. THOMPSON, 1985. Emergence, longevity and breeding area fidelity in *Coenagrion puella* (L.) (Zygoptera: Coenagrionidae). *Odonatologica* 14: 279-286.
- BENNETT, S. & P.J. MILL, 1993. Larval development and emergence in *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Odonatologica* 22: 133-145.
- BEYNON, T.G., 1995. *Leucorrhinia dubia* (Vander Linden) at Shooters Pool, Chartley Moss, Staffordshire, in 1994. *J. British Dragonfly Soc.* 11: 1-9.
- BISWAS, V., A. BEGUM, M.A. BASHIR & S.A. BEGUM, 1994. Emergence pattern of some dragonfly (Odonata: Anisoptera) larvae under the laboratory condition. In: V.K. Srivastava, [Ed.], *Advances in oriental odonatology*, pp. 23-30, Cherry Publs, Allahabad.
- CORBET, P.S., [Ed.], 1988. A discussion focusing on the seasonal ecology of *Pantala flavescens* in the Indian subcontinent. *Soc. Int. Odonatol. rapid Comm. (Suppl.)* 8: viii + 24 pp.
- CORBET, P.S., 1999. *Dragonflies: behaviour and ecology of Odonata*. Harley, Colchester.
- CORBET, P.S. & R. HOESS, 1998. Sex ratio of Odonata at emergence. *Int. J. Odonatol.* 1: 99-118.
- CORDERO, A., 1995. Vertical stratification during emergence in Odonata. *Notul. odonatol.* 4: 103-105.
- CROWLEY, P.H. & F. JOHANSSON, 2002. Sexual dimorphism in Odonata: age, size, and sex ratio at emergence. *Oikos* 96: 364-379.
- DOI, H., 2008. Delayed phenological timing of dragonfly emergence in Japan over five decades. *Biol. Lett.* 4: 388-391.
- DOLNY, A., P. DROZD, M. PETRIKOVA & F. HARABIS, 2010. Sex ratios at emergence in populations of some central European Gomphidae species (Anisoptera). *Odonatologica* 39: 217-224.
- DUNKLE, S.W., 1985. Larval growth in *Nasiaeschna pentacantha* (Rambur) (Anisoptera: Aeshnidae). *Odonatologica* 14: 29-35.
- FOSTER, S.E. & D.A. SOLUK, 2004. Evaluating exuvia [sic] collection as a management tool for the federally endangered Hine's emerald dragonfly, *Somatochlora hineana* Williamson (Odonata: Corduliidae). *Biol. Conserv.* 18: 15-20.
- INDEN-LOHMAR, C., 1997. *Sukzession, Struktur und Dynamik von Libellenpopulationen an Kleingewässern, unter besonderer Berücksichtigung der Ökologie von Aeshna cyanea (Müller, 1764)*. Diss. Math.-naturw. Fak. Friedrich-Wilhelms-Univ., Bonn.
- INOUE, K., 1979. Review of the Japanese dragonflies, 6. *Gracile* 24: 1-20. — [Jap.].
- KIAUTA, B., 1969. Sex chromosome and sex determining mechanism in Odonata, with a review of the cytological conditions in the family Gomphidae, and references to the karyotypic evolution in the order. *Genetica* 40: 127-157.
- KUMAR, A., 1976. Biology of Indian dragonflies with special reference to seasonal regulation and larval development. *Bull. Ent.* 17: 37-47.
- KUMAR, A., 1984. On the life history of *Pantala flavescens* (Fabricius) (Libellulidae: Odonata). *Ann. Ent.* 2: 45-50.
- KURATA, M., 1971. The life history of *Gomphus melaenops* (Gomphidae). *Tombo* 14: 6-11. — [Jap.].
- LUTZ, P.E., 1968. Effect of temperature and photoperiod on larval development in *Lestes eurinus* (Odonata: Lestidae). *Ecology* 49: 637-644.
- MICHIELS, N.K. & A.A. DHONDT, 1989. Effects of emergence characteristics on longevity and maturation in the dragonfly *Sympetrum danae* (Anisoptera: Libellulidae). *Hydrobiologia* 171: 149-158.
- MOORE, N.W. & P.S. CORBET, 1990. Guidelines for monitoring dragonfly population. *J. Brit. Dragonfly Soc.* 6: 21-23.
- PAULSON, D.R., 1966. *The dragonflies (Odonata: Anisoptera) of southern Florida*. Ph.D. thesis. Univ. Miami, Coral Gables/FL.
- POYYAMOLI, G. & T.J. PANDIAN, 1985. Studies on diel emergence pattern of some tropical drag-

- onflies. *Proc. 1st Indian Symp. Odonatol.*, Madurai, pp. 159-165.
- PURSE, B.V. & D.J. THOMPSON, 2003. Emergence of the damselfies, *Coenagrion mercuriale* and *Ceriagrion tenellum* (Odonata: Coenagrionidae), at the northern range margins, in Britain. *Eur. J. Ent.* 100: 93-99.
- RICHTER, O., F. SUHLING, O. MÜLLER & D. KERN, 2008. A model for predicting the emergence of dragonflies in a changing climate. *Freshw. Biol.* 53: 1868-1880.
- TROTTIER, R., 1966. The emergence and sex ratio of *Anax junius* Drury (Odonata: Aeshnidae) in Canada. *Can. Ent.* 98: 794-798.
- TROTTIER, R., 1973. Influence of temperature and humidity on the emergence behavior of *Anax junius* (Odonata: Aeshnidae). *Can. Ent.* 105: 975-984.
- UBUKATA, H., 1973. Life history and behavior of the corduliid dragonfly, *Cordulia aenea amurensis* Selys I. Emergence and pre reproductive period. *J. Fac. Sci. Hokkaido Univ.* (VI) 19: 251-269.
- UBUKATA, H., 1981. Survivorship curve and annual fluctuations in the size of emerging population of *Cordulia aenea amurensis* Selys (Odonata: Corduliidae). *Jap. J. Ecol.* 31: 335-346.
- UBUKATA, H., 1984. Oviposition site selection and avoidance of additional mating by female of the dragonfly *Cordulia aenea amurensis* Selys (Odonata: Corduliidae). *Res. Pop. Ecol.* 26: 285-301.
- WAAGE, J.K., 1980. Adult sex ratio and female reproductive potential in *Calopteryx* (Zygoptera: Calopterygidae). *Odonatologica* 9: 217-320.
- WORTHEN, W.B., 2010. Emergence-site selection by the dragonfly *Epitheca spinosa* (Hagen) *SEast. Naturalist* 9: 251-258.

**THE REPRODUCTIVE BIOLOGY AND DAILY ACTIVITY
PATTERNS OF *ISCHNURA HETEROSTICTA* (BURMEISTER)
IN EASTERN AUSTRALIA
(ZYGOPTERA: COENAGRIONIDAE)**

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The reproductive behaviour was observed at a pond in Fig Tree Pocket, Brisbane, Australia, from Oct. 2010 to Jan. 2011. In total, 769 individuals were marked in the field for observations pertaining to the daily activity patterns and reproductive cycle of this sp. Forty-one *I. heterosticta* pairs were collected and kept in the laboratory for detailed observations of the reproductive behaviours, copulation duration and oviposition, and to determine the duration of larval development. It started to form mating pairs from ca 5:00 to 9:00 am, foraged from ca 9:00 am to 13:00 pm, and finally ♀♀ oviposited mainly from ca 13:00 pm to 16:30 pm. Oviposition usually occurred in the following days after mating. Mating pairs formed the tandem position for about 13 s, then copulated in the wheel position on average for 195 min, and upon completion of insemination formed a tandem position again for about 12 s. On average, ♀♀ spent 145 min in actual oviposition, laying several hundred eggs on floating vegetation. Ovipositing ♀♀ were not guarded by ♂♂. The eggs hatched within 10 to 21 days, and the larvae took 3 to 5 months to develop into adults.

INTRODUCTION

An understanding of the biology of an animal is crucial for discerning the roles the organism plays in the ecosystems it is a part of. Its reproductive biology is particularly important since it involves sexual selection, which plays an important role in determining the fitness of a species, and an indepth understanding of the reproductive biology of a species can thus contribute to the development of more

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comprehensive life-history models and is useful for elucidating phylogenetic relationships.

In odonates, sexual selection plays an important role in adaptive radiation (SVENSON et al., 2006). Odonates have complex reproductive behaviour displays (CORBET, 1999) and members of the genus *Ischnura* have been shown to exhibit a variety of different reproductive behaviours (PAULSON & CANNINGS, 1980; ROBERTSON, 1985; FINCKE, 1987; MILLER, 1987a; CORDERO, 1989). In general, they tend to have long mating durations, with the exact duration varying greatly between and within species (Tab. I). Females of *Ischnura* spp. usually mate several times during their life span.

Currently, three *Ischnura* species are known to occur naturally in Australia. Both *I. heterosticta*, and *I. aurora* have a wide distribution throughout Australia and tend to prefer still water habitats (THEISCHINGER & HAWKING, 2006). *I. pruinescens*, on the other hand, is limited to the northern and eastern parts of Australia, where it inhabits riverine habitats (THEISCHINGER & HAWKING, 2006).

I. heterosticta exhibits female-limited polymorphism, which is a common feature of the genus (ASKEW, 1988). The thorax and tip of the abdomen of males are blue, with the remainder of their abdomen being of black and brownish colour on the dorsal and ventral sides, respectively (Fig. 1). The females, on the other hand, have four types of colouration. Andromorph females have exactly the same blue colouration pattern as the males. The other three types of females are heteromorphs and their colouration differs quite strikingly from that of the andromorphs. The heteromorphs can be categorized as: green, intermediate and grey heteromorphs, based on the colouration on their thoraces and abdomens (Fig. 1).

There are only a few previous studies that focus on the biology of *I. heterosticta*. One study showed that blue *I. heterosticta* morphs, both males and females, could partially change their body colouration in response to temperature variations (O'FARREL, 1964). A series of other studies demonstrated that the larvae

Table I
Copulation duration in *Ischnura*

Species	Range (min)	Mean (SD) (min)	Reference
<i>Ischnura elegans</i>	--	324 (90)	MILLER, 1987a
<i>Ischnura gemina</i>	--	43.6 (27.4)	HAFERNIK & GARRISON, 1986
<i>Ischnura graellsii</i>	38-329	189.2 (8.4)	CORDERO, 1989
<i>Ischnura heterosticta</i>	75-250	194 (45)	This study
<i>Ischnura ramburii</i>	90-400	202 (114)	ROBERTSON, 1985
<i>Ischnura senegalensis</i>	93-433	395.3 (11.6)	SAWADA, 1995
<i>Ischnura verticalis</i>	--	43.5 (2)	FINCKE, 1987

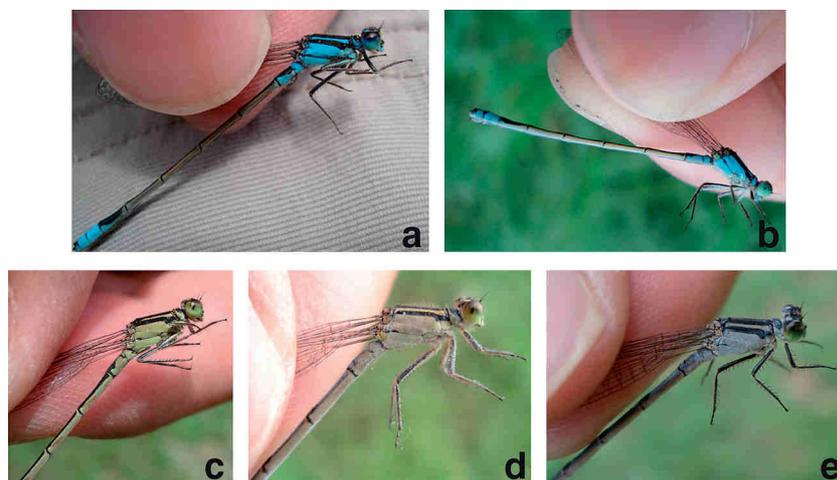


Fig. 1. The different colour morphs of *Ischnura heterosticta*. Top row: (a) a blue male; – (b) an andromorph blue female; – bottom row: (c) a heteromorph green female; – (d) a heteromorph intermediate female; – (e) a heteromorph grey female.

are capable of tolerating salinity up to 45–47 mScm⁻¹ electrical conductivity (KEFFORD et al., 2003, 2004, 2006). The reproductive behaviour and general biology of this species are thus still poorly investigated. Therefore, here we present the first description of the reproductive biology and daily activity patterns of *I. heterosticta* in eastern Australia.

MATERIAL AND METHODS

The in situ observations were made at a large pond, with an area of approximately 600 m², located inside Biambi Yumba Park, Fig Tree Pocket, Brisbane, Australia. The study was carried out from October 2010 to January 2011, five days a week, from 5:00 AM to 17:00 PM. In this habitat *I. heterosticta* coexists with *Agriocnemis pygmaea*, *Austroagrion watsoni*, *Austrolestes leda*, *Ceriagrion aeruginosum*, *Hemicordulia tau*, *I. aurora*, *Pseudagrion microcephalum*, and *Xanthagrion erythroneurum*. Adult *I. heterosticta* were captured and marked, by writing a distinctive number on the left hind-wing, with a fine lead-free water-proof black ink marker pen, after which the insect was released. Observations of free-flying individuals were conducted using binoculars, which allowed identification of individuals via the numbers on their wings. All activities were recorded, with particular focus on reproductive behaviours.

Forty-one *I. heterosticta* pairs were taken to the laboratory at the University of Queensland to make more detailed observations pertaining to the reproductive behaviours and copulation durations of this species, which are not possible in the field due to the distance between observer and insect. Pairs were kept in cages (45 × 45 × 45 cm), with a tray containing water and moist soil in the bottom of the cage and artificial plants for perching. All reproductive behaviour was recorded and subsequently analyzed with respect to duration and sequence of the behaviours.

To determine the average number of eggs laid after mating, 18 of the females were placed individually in small plastic containers (10 × 5 × 3 cm), which had a sheet of wet filter paper at the bottom for

oviposition. After the females completed oviposition, the number of eggs laid was recorded and each container was filled with water to a depth of about 1 cm. The containers were kept at room temperature, with 12:12 hr light-dark cycles, to record the incubation period until hatching.

The eggs were used to investigate the duration of larval development. This was conducted in the laboratory, as it is impossible to track and observe *I. heterosticta* larvae in the field. Once the eggs hatched, the larvae were carefully isolated, and reared individually in separate containers to prevent cannibalism. Small rocks and some vegetation (*Lemna* sp.) were placed inside the containers to create shelters for the larvae. Brine shrimps (*Artemia* sp.) were used as food for the larvae while they were small; with increasing instar size they were fed water fleas or mosquito larvae. Time to full development was recorded.

RESULTS

DAILY ACTIVITIES

Seven-hundred and sixty-nine *I. heterosticta* (387 males, 382 females) were captured, marked and released for observation. The major period during which *I. heterosticta* was observed mating was early morning, immediately after sunrise, from ca. 5:00 to 9:00 am (Tab. II). Individuals that failed to form mating pairs, spent this time foraging or resting on vegetation at the water's edge. From ca. 9:00 am to 13:00 pm, most individuals were foraging or feeding, while resting on vegetation around the water's edge or on the water surface. Occasionally, mating pairs were still observed during this period (14 cases in a three months observation period). Some males occupied floating vegetation as temporary territories. They patrolled and defended this area by chasing/attacking any intruders. However, not every male showed such behaviour and none of them occupied the same spot repeatedly or constantly for an extended period of time. In the afternoon, from ca. 13:00 to 16:30 pm, most females started to oviposit. Males showed no female-guarding behaviour while females oviposited, and tended to spend the time foraging or continued to defend the temporary territories. After 16:30 pm, most individuals sought shelter in the vegetation along the pond to rest.

Table II
Daily activities of *Ischnura heterosticta* observed in the field

Time	Major activities	Other activities
5:00-9:00	Mating	Foraging
9:00-13:00	Foraging	Mating; males patrolling and defending temporary floating territories
13:00-16:30	Oviposition (females) Foraging (males)	Males patrolling and defending temporary territories

MATING BEHAVIOUR

After dawn, males sought out females, usually heteromorphs. When a male located a female, he grabbed her at the wing basis with his legs (Fig. 2a) and then clasped the female's prothorax with his anal appendage to form the tandem position (Fig. 2b, c). Courtship behaviours were never observed. The precopulatory tandem position lasted for 3 to 36 s (mean \pm SD: 12.8 ± 7.9 s), after which the male swung the female's abdomen up and down, by means of wing beating, to initiate genital touching. If the female was receptive, she swung her abdomen forward and upward, to initiate genital touching and copulation (Fig. 2d). Once copulation was initiated, the male moved his abdomen repeatedly forward and upward during the first half of the copulation period. This behaviour is believed to be associated with sperm removal (MILLER, 1987b; CORDERO & MILLER, 1992; SAWADA, 1995; TAJIMA & WATANABE, 2010). Mating pairs maintained this wheel position and remained at the same location most of the time. This stage occupied the largest proportion of the copulation time, which lasted a total of 75-250 min (mean \pm SD: 195 ± 45 min) (Fig. 2d).

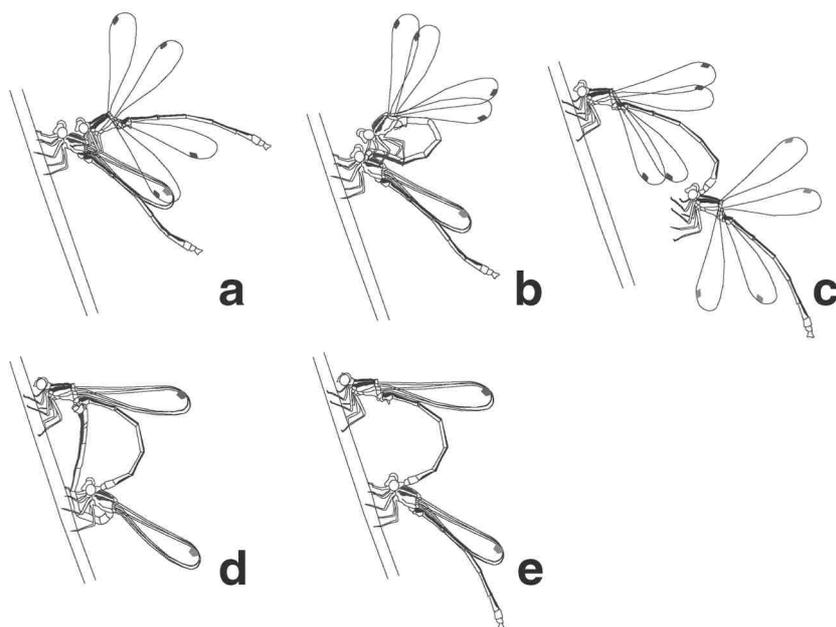


Fig. 2. Reproductive behaviour of *Ischnura heterosticta*: (a) male grabs wing base of female to immobilize her; – (b) male clasps female with anal appendage; – (c) mating pair forms tandem position; – (d) mating pair forms wheel position for copulation; – (e) mating pair returns to tandem position after copulation.

When they were disturbed by other males, or by avian or anthropogenic activities, the mating pair flew away for a distance of 1 to 10 m. Other males, irrespective of whether they were previously observed to defend temporary territories or not, always showed aggressive behaviour towards mating pairs; this often involved physical contact. Such aggressive behaviour persisted until the mating pair left the area or until the attacking male retreated. While in the wheel position, the mating pair usually perched on vegetation along the water's edge, and rarely rested on the water surface. Upon completion of copulation, they formed the tandem position again for 8 to 17 s (mean \pm SD: 12.4 ± 2.5 s) (Fig. 2e), after which the male and female separated.

OVIPOSITION AND LARVAL DEVELOPMENT

Oviposition took place mainly from ca 13:00 to 16:30 pm, although a few females were observed to oviposit earlier in the morning. Females, perching on floating vegetation, were observed embedding eggs among the roots of the vegetation. Ovipositing females very often altered oviposition location, and on average only remained at the same location for 100 to 476 s (mean \pm SD: 170 ± 110.4 s) before moving to the next spot to continue laying eggs. The entire oviposition process of every female lasted for 45 to 212 min (mean \pm SD: 145 ± 51 min). Females that mated in the morning were unlikely to oviposit that afternoon, and most probably only started oviposition during the following few days. Unlike many other *Ischnura* species (CORBET, 1999), *I. heterosticta* males showed no post-copulatory guarding behaviour and thus ovipositing females were often subjected to some harassment (S.-c. Huang & J. Reinhard, in preparation).

Under laboratory condition, oviposition was recorded from 18 females. Each female laid 100 to 876 eggs (mean \pm SD: 589 ± 234) and the eggs hatched, under laboratory conditions, within 10 to 21 days (mean \pm SD: 14.3 ± 5.1 days). The larvae were transparent and usually hidden underneath the sheet of filter paper provided or clung to the roots of the vegetation. Twenty-one of the larvae developed successfully into adults after three to five months (mean \pm SD: 131 ± 45 days).

DISCUSSION

The long mating period observed in *I. heterosticta* is a common trait of this genus (Tab. I). It has been shown that the copulation duration can vary due to changes in the densities of the damselfly populations or the localities they inhabit (MILLER, 1987b; COOPER et al., 1996). The mating duration in *I. heterosticta* also correlated negatively with the time since mating was initiated as described in *I. graellsii* (CORDERO, 1990). This behaviour is important for sperm competition, because longer copulation is a mate-guarding strategy to prevent the females from

re-mating before oviposition (CORDERO, 1990).

Sperm competition plays an important role in sexual selection (PARKER, 1970; SMITH, 1984), particularly in *Ischnura* species. Based on the evidence of sperm precedence comparisons among different species, it is clear that sperm displacement ability is widespread among temperate-zone zygopterans (WAAGE, 1986). SAWADA (1995) found that *I. senegalensis* started to remove the sperm from former matings within the first hour after copulation was initiated and executed sperm insemination one minute before the copulation ended. As for *I. heterosticta*, in the first half of the copulation period, males swung their abdomens upward and forward more often and we believe that they were displacing the sperm of other competitors during this period. However, we are not certain about the exact amount of time spent on sperm removal and insemination.

WAAGE (1984) defined postcopulatory behaviours into three types: oviposition in tandem, non-contact guarding, and the female ovipositing alone. Some coenagrionid species oviposit in tandem but in most *Ischnura* species this is not the case. *I. heterosticta* females oviposit without male-guarding behaviour. When females oviposited, they were subjected to male harassment, which varied according to their colouration (S.-c. Huang & J. Reinhard, in preparation). The females changed oviposition localities very often, which is more than likely a strategy to reduce the risk of predation on the eggs and larvae by aquatic predators. It could also be a means of reducing cannibalism among siblings when they hatch. Under laboratory conditions, the eggs hatched within three weeks and the larvae turned into adults after three to five months. Due to the short larval development period, and because females mate and oviposit multiple times, *I. heterosticta* can be observed during the entire year. However, their major flight season is from October to March.

Climatic factors play important roles in the reproductive behaviour of *I. heterosticta*. Wind conditions, in particular, had a great impact on the willingness to mate among individuals. When the weather was windy, few individuals were in flight and only a few mating pairs were observed in the early morning. We suspect that due to its small body size, *I. heterosticta* has difficulties counterbalancing strong winds, which means that, under such conditions, flight would require more energy and there would be a greater risk of injury. Rainfall was the second major factor that impeded the activities of *I. heterosticta*. They sought shelter among vegetation while weather conditions were unsuitable for them to be active.

This study is the first detailed description of *I. heterosticta* reproductive biology and daily activity patterns. Many of the behaviours observed are in line with those described from other Ischnuran species (Tab. I). It would be interesting to investigate whether and how female polymorphism is linked to different reproductive strategies and sexual selection in this species.

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REFERENCES

- ASKEW, R.R., 1988. *The dragonflies of Europe*. Harley Books, Martins.
- CORBET, P.S., 1999. *Dragonflies: behavior and ecology of Odonata*. Cornell Univ. Press, New York.
- COOPER, G.P., W.H. HOLLAND & P.L. MILLER, 1996. Captive breeding of *Ischnura elegans* (Vander Linden): observations on longevity, copulation and oviposition (Zygoptera: Coenagrionidae). *Odonatologica* 25: 261-273.
- CORDERO, A., 1989. Reproductive behaviour of *Ischnura graellsii* (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica* 18: 237-244.
- CORDERO, A., 1990. The inheritance of female polymorphism in the damselfly *Ischnura graellsii* (Rambur) (Odonata: Coenagrionidae). *Heredity* 64: 341-346.
- CORDERO, A. & P.L. MILLER, 1992. Sperm transfer, displacement and precedence in *Ischnura graellsii* (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* 30: 261-267.
- FINCKE, O.M., 1987. Female monogamy in the damselfly *Ischnura verticalis* Say (Zygoptera: Coenagrionidae). *Odonatologica* 16: 129-143.
- HAFERNIK, J.E. & R.W. GARRISON, 1986. Mating success and survival rate in a population of damselflies: results at variance with theory? *Am. Nat.* 128(3): 353-356.
- KEFFORD, B.J., P.J. PAPAS, L. METZELING & D. NUGEGODA, 2004. Do laboratory salinity tolerances of freshwater animals correspond with their field salinity? *Envir. Pollut.* 129: 355-362.
- KEFFORD, B.J., P.J. PAPAS & D. NUGEGODA, 2003. Relative salinity tolerance of macroinvertebrates from the Barwon River, Victoria, Australia. *Mar. Freshw. Res.* 54: 755-765.
- KEFFORD, B.J., L. ZALIZNIAK & D. NUGEGODA, 2006. Growth of the damselfly *Ischnura heterosticta* is better in saline water than freshwater. *Envir. Pollut.* 141: 409-419.
- MILLER, P.I., 1987a. An examination of the prolonged copulations of *Ischnura elegans* (Vander Linden) (Zygoptera: Coenagrionidae). *Odonatologica* 16: 37-56.
- MILLER, P.I., 1987b. Sperm competition in *Ischnura elegans* (Vander Linden) (Zygoptera: Coenagrionidae). *Odonatologica* 16: 201-207.
- O'FARRELL, A.F., 1964. On physiological colour change in some Australian Odonata. *J. ent. Soc. Aust.* 1: 5-12.
- PARKER, G.A., 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45: 525-567.
- PAULSON, D.R. & R.A. CANNINGS, 1980. Distribution, natural history and relationships of *Ischnura erratica* Calvert (Zygoptera: Coenagrionidae). *Odonatologica* 9: 147-153.
- ROBERTSON, H.M., 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Anim. Behav.* 33: 805-809.
- SAWADA, K., 1995. Male's ability of sperm displacement during prolonged copulations in *Ischnura senegalensis* (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica* 24: 237-244.
- SMITH, R.L., 1984. *Sperm competition and the evolution of animal mating systems*. Academic Press, New York/London.
- SVENSSON, E.I., F. EROUKHMANOFF & M. FRIBERG, 2006. Effects of natural and sexual selection on adaptive population divergence and premating isolation in a damselfly. *Evolution* 60: 1242-1253.
- TAJIMA, Y. & M. WATANABE, 2010. Sperm transfer process in the non-territorial *Ischnura asiatica*

- (Brauer) during copulation (Zygoptera: Coenagrionidae). *Odonatologica* 39: 253-258.
- THEISCHINGER, G. & J. HAWKING, 2006. *The complete field guide to dragonflies of Australia*. CSIRO Publishing, Collingwood.
- WAAGE, J.K., 1984. Sperm competition and the evolution of Odonata mating systems. In: R.L. Smith, [Ed.], *Sperm competition and the evolution of animal mating systems*, pp. 251-290, Academic Press, New York/London.
- WAAGE, J.K., 1986. Evidence for widespread sperm displacement ability among Zygoptera (Odonata) and the means for predicting its presence. *Biol. J. Linn. Soc.* 28: 285-300.

**PATTERNS OF MITOCHONDRIAL AND WING
MORPHOLOGICAL DIFFERENTIATION IN TAIWANESE
POPULATIONS OF *PSOLODESMUS MANDARINUS*
McLACHLAN (ZYGOPTERA: CALOPTERYGIDAE)**

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To investigate the patterns of molecular and morphological differentiation, the mitochondrial cytochrome oxidase I and 16S ribosomal DNA genes and wing morphology data were analyzed. Both phylogenetic and population genetic analyses revealed two lineages, an Eastern and a Western lineage existing on each side of the longitudinal Central Mountain Range. For wing traits, the latitudinal clines mainly altered across the populations in northern Taiwan and the transition zone was broad. For ♀ wing size, however, the latitudinal cline shifted at 24.19 degrees N latitude, which is close to the current criteria (24.33 degrees N latitude line) for dividing 2 geographical ssp., *P. m. mandarinus* and *P. m. dorothea*.

INTRODUCTION

Psolodesmus is a small genus of Calopterygidae with only one species *P. mandarinus*, which is found on some East Asia Pacific islands. The type, a single male, was found at 'Amoy' (now Xiamen) in China by McLACHLAN (1870). Because of no confirmed records from mainland China since 1870, HÄMÄLÄINEN (2004) suggested that the type specimen was probably collected from Taiwan, and shipped to Europe from Amoy. WILLIAMSON (1904) described *P. dorothea* from Taiwan, distinguished from *P. mandarinus* by a less extensive apical blackish area of the wings and a sub-basal area that was always clear hyaline. However, CHEN (1950) concluded that *mandarinus* and *dorothea* were the same

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species, without any separating character on the anal appendages and penile organs. However, the two wing colour forms may be geographical subspecies, *P. m. mandarinus* and *P. m. dorothea*, separated by the 24.33 degrees north line of latitude, with *P. m. mandarinus* in northern Taiwan, and *P. m. dorothea* in central and southern Taiwan. LIEFTINCK et al. (1984) recommended that the transition zone between the two subspecies should be better established.

Recently, the mitochondrial genes cytochrome oxidase I (COI) and 16S ribosomal DNA (16S) have often been used to reassess the taxonomic status at genus and species levels in Calopterygidae (MISOF et al., 2000; MULLEN & ANDRES, 2007). The COI gene is believed to provide a historic signal of past demographic and geographic changes. It has become a favoured gene for studying the genetic consequences of climatic oscillations in the Quaternary (HEWITT, 2004). Other genetic markers have also been used in Calopterygidae, such as nuclear small subunit (SSU) ribosomal DNA, internal transcribed spacers (ITS) (WEEKERS et al., 2001; HAYASHI et al., 2004; DUMONT et al., 2005, 2007) and amplified fragment length polymorphism (AFLP) (SVENSSON et al., 2004; SADEGHI et al., 2010).

In this study, we investigate the patterns of mitochondrial and wing morphological differentiation in Taiwanese populations of *Psolodesmus mandarinus*, and examine subspecies distribution, wing morphology and molecular population divergence.

MATERIAL AND METHODS

SPECIMENS COLLECTION AND USAGE – Adult specimens were collected from 27 locations throughout Taiwan and immediately preserved in 95% ethanol except the wings. We used 60 specimens from 20 locations for DNA sequencing; thus a total of three mitochondrial sequences from each location was obtained. The specimens for morphological analysis consisted of 200 males from 20 locations and 124 females from 25 locations. Information for the specimens used in DNA sequencing and morphological analysis is given in Table I and Figure 1.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING – Genomic DNA was extracted from muscular tissue of the synthorax using the protocol of the Puregene™ DNA isolation kit type D-5000A (Gentra System INC., BIOzym, Netherlands). The mitochondrial partial 16S ribosomal DNA gene sequence was amplified by polymerase chain reaction (PCR) with the universal primer sets, LR-J-12887 (5'-CCGGTTTGAAGTCAAGATCATGT-3') and LR-N-13398 (5'-CGCCT-GTTTAACAAAACAT-3') (SIMON et al., 1994). The PCR reaction program was initialized at 94 °C for 2 min, followed by 35 cycles with 30 s 94 °C, 30 s 50 °C, 40 s 72 °C and finished at 72 °C for 10 min. The partial COI gene sequence was amplified by PCR with the universal primer sets, LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGAC-CAAAAATCA-3') (FOLMER et al., 1994). The procedure of the PCR program was initialized at 94 °C for 2 min, followed by 35 cycles with 30 s 94 °C, 30 s 45 °C, 40 s 72 °C and finished at 72 °C for 10 min. PCR products were purified with the Micro-Elute DNA Clean/Extraction kit (Gene Mark, Taiwan) and sequenced on an ABI PRISM 3730 DNA Analyzer (Applied Biosystems, CA).

MOLECULAR PHYLOGENETIC ANALYSIS – All sequences were aligned using the Clustal×1.18 program (THOMPSON et al., 1997) and manually edited with the GeneDoc program (NICHOLAS et al., 1997). The combinability of the 16S and COI gene regions was tested with the parti-

tion homogeneity test (FARRIS et al., 1995) by PAUP – 4.0b10 (SWOFFORD, 2002). The partition homogeneity test revealed significant congruence ($p = 0.795$), so two gene regions were combined for phylogenetic analysis. The method of Maximum Likelihood (ML) was selected to construct the phylogenetic tree (FELSENSTEIN, 1981) by PhyML online (GUINDON & GASCUEL, 2003). MrMODELTEST version 2.3 (NYLANDER, 2004) identified the HKY+G model as the best-fit model for the ML phylogenetic analysis. The robustness of the ML phylogenetic tree was assessed by 1,000 bootstrap replicates (FELSENSTEIN, 1985). Two related species, *Mnais tenuis* Oguma and *Matrona cyanoptera* Hämäläinen and Yeh from Taiwan were used as outgroups.

POPULATION GENETIC DATA ANALYSIS – To understand the levels of genetic diversity in different phylogenetic groups, the genetic diversity of the COI gene was quantified by haplotype number (S), haplotype diversity (h)

$$h = \frac{n}{n-1} \left(1 - \sum_{i=1}^l p_i^2 \right) \quad (1)$$

(where p_i is the sequence frequency of the i th of l haplotypes and n is the sample size) and nucleotide diversity (π)

$$\pi = \frac{n}{n-1} \sum_{i \neq j} p_i p_j \pi_{ij} \quad (2)$$

(where p_i and p_j are the sequence frequencies of the i th and j th haplotypes and π_{ij} is the number of nucleotide differences per nucleotide site between the i th and j th haplotypes). We estimated the nucleotide differentiation between phylogenetic groups by the fixation index (F_{st})

$$F_{st} = 1 - \frac{H_w}{H_b} \quad (3)$$

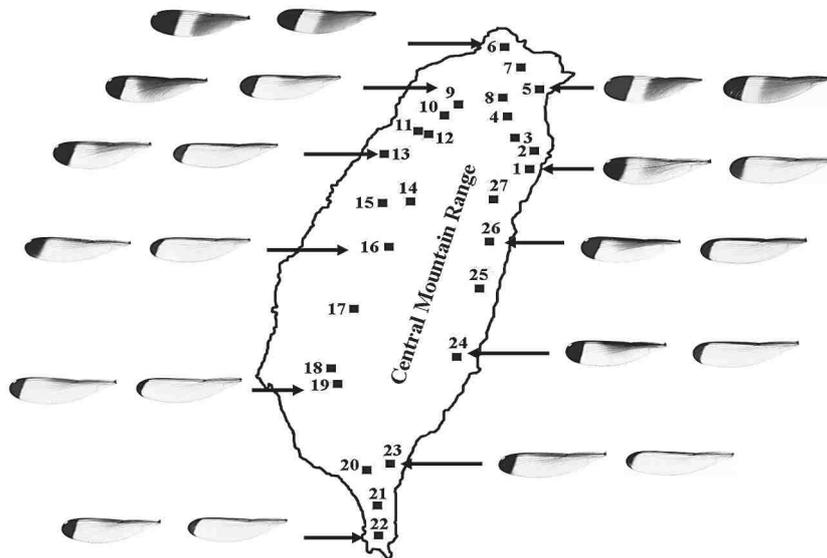


Fig. 1. Map of sampling locations, and the wing color phenotypes on left forewings (left, female; right, male). Location codes are the same as those in Tab. 1.

Table I
Specimen information about collection locations, taxonomic status, number of males (nm) and females (nf) using in morphological analysis, number of sequenced individuals (ns), and haplotypes of 16S, COI, and 16S+COI in these sequenced individuals

Code	Locality	Location	Subspecies	nm	nf	ns	16S haplotype	COI haplotype	16S+COI haplotype
1	Nanao	24.38N, 121.78E	<i>P. m. mandarinus</i>	10	2	3	S1, S1, S2	C1, C1, C2	P1, P1, P2
2	Xinao	24.48N, 121.82E	<i>P. m. mandarinus</i>		4				
3	Hanxi	24.60N, 121.69E	<i>P. m. mandarinus</i>	10	5	3	S1, S1, S1	C1, C1, C1	P1, P1, P1
4	Yuanshan	24.75N, 121.65E	<i>P. m. mandarinus</i>	10	4	3	S1, S1, S1	C1, C1, C3	P1, P1, P3
5	Daxi	24.94N, 121.87E	<i>P. m. mandarinus</i>	10	6	3	S1, S1, S1	C1, C1, C4	P1, P1, P4
6	Shimen	25.26N, 121.58E	<i>P. m. mandarinus</i>	10	6	3	S1, S1, S1	C1, C1, C1	P1, P1, P1
7	Pingxi	25.04N, 121.72E	<i>P. m. mandarinus</i>	10		3	S1, S1, S1	C1, C1, C1	P1, P1, P1
8	Wulai	24.82N, 121.58E	<i>P. m. mandarinus</i>	10	3	3	S1, S1, S1	C1, C1, C1	P1, P1, P1
9	Xikuo	24.80N, 121.29E	<i>P. m. mandarinus</i>	10	6	3	S1, S1, S1	C1, C1, C5	P1, P1, P5
10	Guanxi	24.75N, 121.21E	<i>P. m. mandarinus</i>		6				
11	Nanchuang	24.62N, 121.04E	<i>P. m. mandarinus</i>		4				
12	Wufeng	24.59N, 121.11E	<i>P. m. mandarinus</i>	10	5	3	S1, S1, S1	C1, C1, C1	P1, P1, P1
13	Tongluo	24.44N, 120.75E	<i>P. m. mandarinus</i>	10	6	3	S1, S1, S1	C1, C1, C6	P1, P1, P6
14	Lileng	24.15N, 120.97E	<i>P. m. dorothea</i>	10		3	S1, S1, S1	C1, C1, C1	P1, P1, P1
15	Taiping	24.12N, 120.81E	<i>P. m. dorothea</i>		5				
16	Shuili	23.88N, 120.88E	<i>P. m. dorothea</i>	10	6	3	S1, S1, S1	C1, C1, C1	P1, P1, P1
17	Chukou	23.43N, 120.61E	<i>P. m. dorothea</i>	10	6	3	S1, S1, S1	C1, C1, C1	P1, P1, P1
18	Jiaxian	23.07N, 120.61E	<i>P. m. dorothea</i>		4				
19	Liugui	22.97N, 120.65E	<i>P. m. dorothea</i>	10	6	3	S1, S1, S1	C1, C1, C7	P1, P1, P7
20	Chunri	22.42N, 120.76E	<i>P. m. dorothea</i>		6				
21	Mudan	22.14N, 120.80E	<i>P. m. dorothea</i>		6				
22	Manzhou	22.03N, 120.80E	<i>P. m. dorothea</i>	10	5	3	S1, S1, S1	C8, C8, C8	P8, P8, P8
23	Xianglan	22.57N, 120.98E	<i>P. m. dorothea</i>	10	6	3	S1, S1, S1	C8, C9, C9	P8, P9, P9
24	Fuli	23.10N, 121.27E	<i>P. m. dorothea</i>	10	3	3	S3, S3, S3	C10, C10, C10	P10, P10, P10
25	Fengbin	23.65N, 121.49E	<i>P. m. dorothea</i>	10	5	3	S3, S3, S3	C11, C11, C12	P11, P11, P12
26	Tongmen	23.95N, 121.50E	<i>P. m. dorothea</i>	10	2	3	S3, S3, S3	C13, C13, C13	P13, P13, P13
27	Xibao	24.20N, 121.48E	<i>P. m. dorothea</i>	10	5	3	S3, S3, S4	C8, C13, C13	P8, P13, P14

(where H_w is the mean number of differences between the different sequences sampled from the same subpopulation and H_b is the mean number of differences between the different sequences sampled from the two different subpopulations) (HUDSON et al., 1992). DnaSP version 4.10.8 (ROZAS et al., 2003) was used to calculate these values. In addition, gene flow was assessed by the N_m which represents the per-generation effective number of female migrants between pairwise populations. The N_m is estimated by the equation:

$$N_m = \frac{1}{2} \left(\frac{1}{F_{st}} - 1 \right) \quad (4)$$

WING MORPHOLOGICAL ANALYSIS – We measured three morphological characters on the left forewing: the wing size (area) (WS), the percentage of the apical blackish area (ABA%), and the relative transparency of the sub-basal area (RT%) (Fig. 2).

First, we took digital images of the left forewings using an Epson Stylus Photo RX630 scanner and measured wing size (WS) and apical blackish area (ABA) using the TsView 6.0 image processing software. The relative transparency of the sub-basal area (RT%) was measured by a device similar to the apparatus used by BEUKEMA (2004). To standardize the measurement of RT, a square of 5×5 mm of the sub-basal area (below the nodus) was measured (Fig. 2). A microscope light VOLPI Intralux® 5000-1 through a daylight conversion filter to increase the colour temperature of the light to 5500°K was used as the light source. The light intensities with and without a wing were recorded by a photometer TES-1330. Transmitted light was measured on a relative transparency scale of 0 (total dark) to 1 (total light).

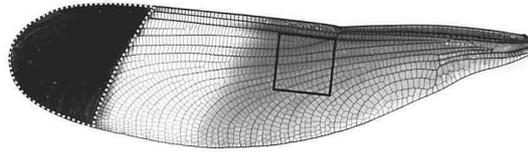


Fig. 2. The apical blackish area (ABA) of left forewing (dotted line), and the detection area for the relative transparency (RT) (open square).

For mathematically describing the latitudinal cline of the wing morphology, we followed the discussion of BARTON & GALE (1993) and assumed that the cline maintained itself by a balance between dispersal and selection, and could be described by a sigmoidal model. We then generated best-fit curves for the clines using the decreasing sigmoidal model (GIBERT et al., 1998),

$$P = P_{\max} + \frac{P_{\min} - P_{\max}}{1 + e^{S_c(x-IP)}} \quad (5)$$

or the increasing sigmoidal model

$$P = P_{\min} + \frac{P_{\max} - P_{\min}}{1 + e^{S_c(x-IP)}} \quad (6)$$

(where P is the expected value of the phenotype at latitude x , P_{\max} is an upper asymptote of the phenotype, P_{\min} is a lower asymptote of the phenotype, IP is the latitude of the inflection point, i.e., the midpoint of the cline and S_c is a constant related to the slope at the inflection point. The cline width of phenotypic traits was observed by the extent of the transition zone between each side of the cline.

RESULTS

DIFFERENTIATION IN MITOCHONDRIAL GENES

Three specimens of *P. mandarinus* from each of 20 locations were sequenced successfully (Tab. I). 515 base pairs of the 16S gene were obtained: three sites

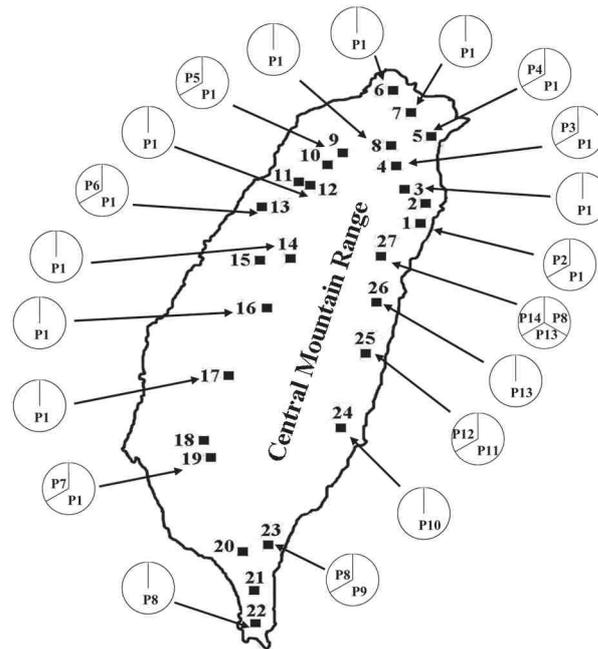


Fig. 3. Frequency distribution of mitochondrial haplotypes (P1-14) among the 20 studied populations. Location codes are the same as those in Tab. I.

from the lower eastern region (Location 22-27, Fig. 3). Moreover, it is worth

were variable (2 transitions, 1 transversion) and four types (S1-4) were identified. Furthermore, 624 base pairs of the COI gene were sequenced; 22 sites were variable (20 transitions, 2 transversions) and 13 types (C1-13) were identified. A total of 14 mitochondrial haplotypes (P1-14) was obtained by combining 16S and COI genetic types (Tab. I). In particular, haplotype P1 was widely distributed in northern and western Taiwan (Fig. 3), and accounted for 60% of all examined specimens. It was not found in specimens

Table II

Sample size (n), number of haplotype (S), haplotype diversity (h), nucleotide diversity (π) in two geographical regions based on COI sequence

Region	Sampling locations	Sample size (n)	Number of haplotype (S)	Haplotype diversity (h)	Nucleotide diversity (π)
Western Taiwan	1, 3-9, 12-14, 16-17, 19, 22-23	48	9	0,43	0,0017
Eastern Taiwan	24-27	12	6	0,79	0,0049

noting that individuals with the haplotype P1 included both *mandarinus* and *dorothea* subspecies (Tab. I).

The molecular phylogenetic tree constructed by the ML method indicated that the 14 haplotypes (P1-14) could be separated into two major clades (Fig. 4), an ‘Eastern Taiwan lineage’ and a ‘Western Taiwan lineage’ with 99% bootstrap value. The Eastern Taiwan lineage consisted of 6 haplotypes (P2, P10-14), and represented most specimens from Location 24-27 on the eastern side of the Central Mountain Range (Fig. 3). The Western Taiwan lineage was composed of 8 haplotypes (P1, P3-9), and represented most specimens from 16 sampling localities in western Taiwan (Fig. 3).

The haplotype diversity (h) and nucleotide diversity (π) of COI gene of eastern Taiwan region was about twice that of western Taiwan region (Tab. II). The fixation index ($F_{st} = 0.82$) showed a geographical differentiation of COI gene between eastern and western Taiwan. Since pairwise N_m value ($N_m = 0.11$) deduced from F_{st} was far smaller than 1, it also revealed that the gene flow between two geographical regions is restricted.

DIFFERENTIATION IN WING MORPHOLOGY

For male populations, the latitudinal clines of the percentage of apical blackish area (ABA%) and the relative transparency (RT%) closely matched a sigmoidal model (Fig. 5 upper figures). The cline midpoint of ABA% was located at 24.74 degrees (near Location 4 and 10) and the transition zone covered almost all sampling sites in northern Taiwan (Location 1-13). The cline midpoint of RT% was

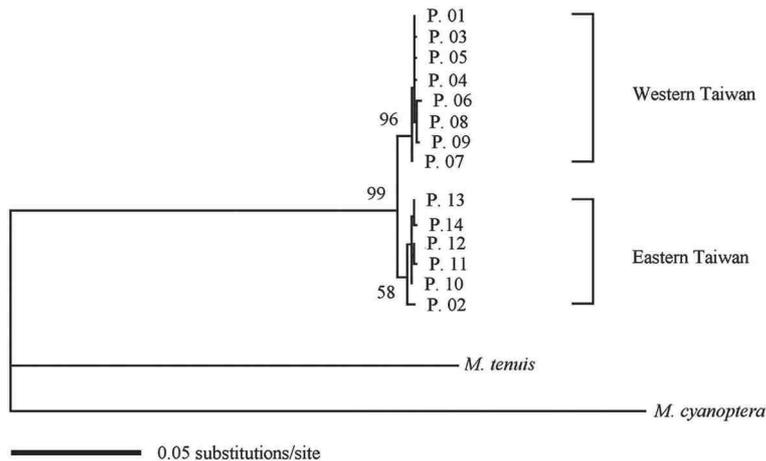


Fig. 4. Maximum likelihood tree based on the mitochondrial haplotypes (P1-14). The numbers above or under the branches are bootstrap values.

similarly located at 24.79 degrees (near Location 4 and 10) and the transition zone also covered almost all sampling sites in northern Taiwan (Location 1-13). For female populations, the latitudinal clines of wing colour traits also closely matched a sigmoidal model (Fig. 5 lower figures). The cline midpoint of ABA% and RT% were located at 25.63 degrees (near Location 6) and 24.79 degrees (near Location 4 and 10) respectively. The transition zones of both ABA% and RT% not only covered the sampling locations in northern Taiwan but also some locations in central Taiwan.

We also found a significant association between the wing size (WS) and latitude across the sampling populations (Fig. 6). Regression coefficients (R^2) for male and female populations were 0.51 and 0.42, respectively, and both were significant at the $p < 0.001$ level. The cline midpoint for male populations was located at 26.46 degrees (north of Location 6) (Fig. 6 left figure). Because WS was slowly increasing with latitude a very broad transition zone was observed across all sampling locations (Fig. 6 left figure). In female populations, the cline midpoint was located at 24.19 degrees (near Location 14 and 27) (Fig. 6 right figure). In this case the transition zone was very narrow, the latitudinal cline shifting dramatically at 24.19 degrees north latitude (Fig. 6 right figure).

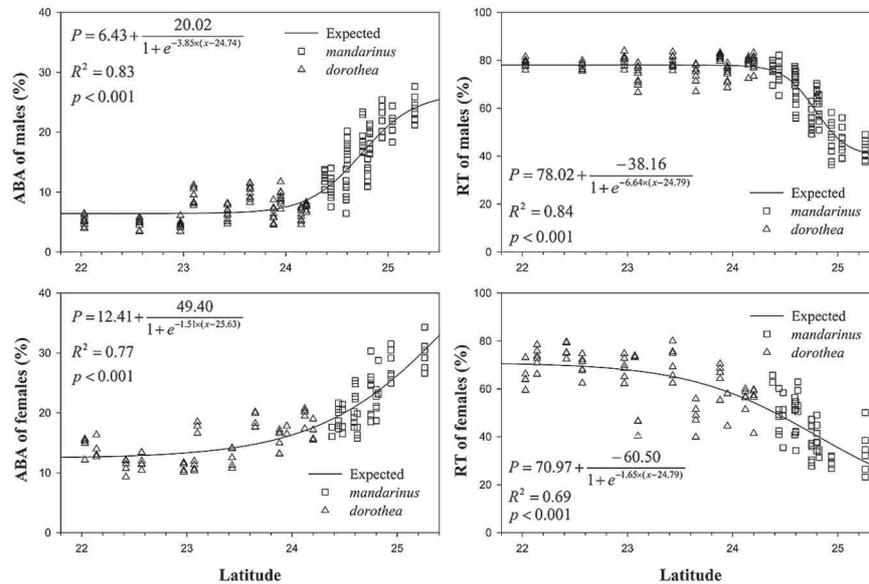


Fig. 5. Clines of apical blackish area (ABA %), and relative transparency (RT %) for males and females taken from two subspecies and a range of latitude (open squares, *P. m. mandarinus*; open triangles, *P. m. dorothea*).

DISCUSSION

CHEN (1950) indicated that two geographical subspecies, *mandarinus* and *dorothea* are separated by about 24.33 north latitude line. However, both molecular phylogeny and population genetics analyses suggested the presence of two lineages, an Eastern and a Western lineage, existing on each side of the longitudinal Central Mountain Range. The prominent Central Mountain Range runs along the north-south longitudinal axis of the island with the highest peak at nearly 4,000m above sea level. It has been suggested that it forms a geographical barrier against gene flow, especially to the lowland animals and plants distributed each side of the Central Mountain Range. For example, there are several cases with a situation similar to that of *P. mandarinus*, such as the cricket *Loxoblemmus appendicularis* (YEH et al., 2004), the stag beetle *Lucanus formosanus* (HUANG & LIN, 2010), the freshwater crab *Candidiopotamon rathbunae* (SHIH et al., 2006), the amphibians *Rana limnocharis* (TODA et al., 1998) and *Sylvirana latouchii* (JANG-LIAW et al., 2008), the bamboo viper *Trimeresurus stejnegeri* (CREER et al., 2001), and the plants *Cyclobalanopsis glauca* (HUANG et al., 2002) and *Hygrophila pogonocalyx* (HUANG et al., 2005). *P. mandarinus* occurs in lowland and hill forest streams up to 1,000 m altitude in Taiwan (LIEFTINCK et al., 1984) and the Central Mountain Range may indeed form a genetic barrier between Eastern and Western lineages.

The genetic diversity indices of eastern Taiwan region ($h = 0.79$, $\pi = 0.0049$) were much higher than those of western Taiwan region ($h = 0.43$, $\pi = 0.0017$). DUMONT et al. (2007) indicated that the genus *Psolodesmus* belonged to a subtropical-tropical taxon rather than a temperate one. It is probable that the populations of *P. mandarinus* were restricted in southern refugia during the Pleistocene glacial period. As climate became warmer, the restricted populations began their outward expansion from southern refugia. It is believed that the different speeds of postglacial colonization were predicted to leave distinct genetic signals. A rap-

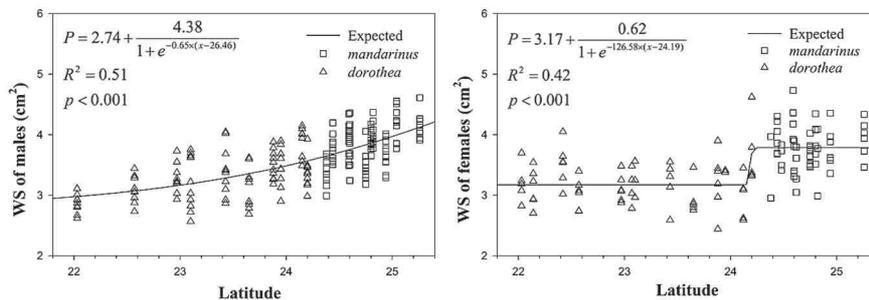


Fig. 6. Clines of wing size (WS) for males and females taken from two subspecies and a range of latitude (open squares, *P. m. mandarinus*; open triangles, *P. m. dorothea*).

id colonization by a pioneer would reduce the genetic diversity and form patches of genotypic homogeneity, but slower expansion by a phalanx would tend to retain diversity (NICHOLS & HEWITT, 1994; IBRAHIM et al., 1996). As mentioned above, the longitudinal Central Mountain Range produced a geographic barrier for the eastern and western populations. The area of the eastern side is far smaller than that of the western side. Therefore, the postglacial colonization of eastern populations may have been restricted by the smaller area, and the dilution of genetic diversity may have been retarded. In contrast, western populations may have expanded rapidly northwards as a result of the larger western plains. Therefore, the smaller degree of genetic diversity in western Taiwan could be explained by the rapid colonization by a pioneer. Furthermore, a patch of genotypic homogeneity was also found in western and northern Taiwan because the haplotype P1 was widespread throughout this area (Fig. 3).

With regard to wing colour, it is impressive that the apical blackish area (ABA%) and the relative transparency (RT%) changed with latitude (Fig. 5). The most important point is that, by combining the molecular and morphological data, we found the rapid change in both pigmentation and wing colour mainly occurring in northern Taiwan during the northerly expansion of the Western lineage. Some studies also have observed that morphological divergence could take place with relatively little molecular divergence during the postglacial population expansion (SEUTIN et al., 1995; MILA et al., 2007). These studies suggested that the advancing populations may encounter a variety of unoccupied habitats with varying selection regimes, which could drive diversification in comparatively short periods of time. Although the reason for driving both pigmentation and wing colour is still unknown, it provides a valuable opportunity to investigate the evolution of wing colour traits and whether there is a link with, for example, parasites resistance, mate quality or species recognition.

CHEN (1950) reported the wing colour differences between *P. m. mandarinus* and *P. m. dorothea*. However, our results revealed that the wing colour traits gradually changed across the populations in central and northern Taiwan. Because of a broad transition zone, it will be hard to determine the distribution limits for the two subspecies. In contrast, the latitudinal cline of female wing size shifted dramatically at the cline midpoint (24.19 degrees) and thus a very narrow transition zone was observed between the central and northern Taiwan locations (Fig. 6 right figure). It is interesting that this is very close to the current criteria (24.33 degrees north latitude line) for dividing the two geographical subspecies, *P. m. mandarinus* and *P. m. dorothea* (CHEN, 1950).

JOHANSSON (2003) suggested that the dramatic latitudinal change of body size at a specific latitude may reflect a shift in generation number per year. It is probable that female generation number alters at 24.19 degrees and thus the life history traits of northern populations may be different from the central and southern populations. It is important to know whether the female life history traits are

associated with wing colour traits to form co-adapted trait complexes, to cope with a different selection regime in northern Taiwan. Furthermore, it would be worth studying the geographical differentiation further using more genetic markers and wing characters, such as pterostigma and wing shape (HAYASHI et al., 2004; SADEGHI et al., 2009).

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REFERENCES

- BARTON, N.H. & K.S. GALE, 1993. Genetic analysis of hybrid zones. *In*: Harrison, R.G., [Ed.], *Hybrid zones and the evolutionary process*. Oxford Univ. Press, New York.
- BEUKEMA, J.J., 2004. Recognition of conspecific females by males of *Calopteryx haemorrhoidalis* (Vander Linden) (Zygoptera: Calopterygidae). *Odonatologica* 33: 147-156.
- CHEN, C.-W., 1950. Systematic notes on the genera *Orolestes* and *Psolodesmus* (Odonata). *Quart. J. Taiwan Mus.* 3: 23-32.
- CREER, S., A. MALHOTRA, R.S. THORPE & W.-H. CHOU, 2001. Multiple causation of phylogeographical pattern as revealed by nested clade analysis of the bamboo viper (*Trimeresurus stejnegeri*) within Taiwan. *Mol. Ecol.* 10: 1967-1981.
- DUMONT, H.J., J.R. VANFLETEREN, J.F. DE JONCKHEERE & P.H.H. WEEKERS, 2005. Phylogenetic relationships, divergence time estimation, and global biogeographic patterns of Calopterygoid damselflies (Odonata, Zygoptera) inferred from ribosomal DNA sequences. *Syst. Biol.* 54: 347-362.
- DUMONT, H.J., A. VIERSTRAETE & J.R. VANFLETEREN, 2007. A revised molecular phylogeny of the Calopteryginae (Zygoptera: Calopterygidae). *Odonatologica* 36: 365-372.
- FARRIS, J., M. KALLERSJO, A.G. KLUGE & C. BULT, 1995. Constructing a significance test for incongruence. *Syst. Biol.* 44: 570-572.
- FELSENSTEIN, J., 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. *J. Mol. Evol.* 17: 368-376.
- FELSENSTEIN, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783-791.
- FOLMER, O., M. BLACK, W. HOEH, R. LUTZ & R. VRIJENHOEK, 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* 3: 294-299.
- GIBERT, P., B. MORETEAU, J.R. DAVID & S.M. SCHEINER, 1998. Describing the evolution of reaction norm shape: body pigmentation in *Drosophila*. *Evolution* 52: 1501-1506.
- GUINDON, S. & O. GASCUEL, 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Syst. Biol.* 52: 696-704.
- HÄMÄLÄINEN, M., 2004. Caloptera damselflies from Fujian (China), with description of a new species and taxonomic notes (Zygoptera: Calopterygoidea). *Odonatologica* 33: 371-398.
- HAYASHI, F., S. DOBATA & R. FUTAHASHI, 2004. Macro- and microscale distribution patterns of two closely related Japanese Mnais species inferred from nuclear ribosomal DNA, ITS sequences and morphology (Zygoptera: Calopterygidae). *Odonatologica* 33: 399-412.
- HEWITT, G.M., 2004. Genetic consequences of climatic oscillations in the Quaternary. *Phil. Trans.*

- R. Soc. Lond. (B)* 359: 183-195.
- HUANG J.-C., W.-K. WANG, C.-I. PENG & T.-Y. CHIANG, 2005. Phylogeography and conservation genetics of *Hygrophila pogonocalyx* (Acanthaceae) based on *atpB-rbcL* noncoding spacer cpDNA. *J. Plant Res.* 118: 1-11.
- HUANG, J.-P. & C.-P. LIN, 2010. Diversification in subtropical mountains: phylogeography, pleistocene demographic expansion, and evolution of polyphenic mandibles in Taiwanese stag beetle, *Lucanus formosanus*. *Mol. Phylog. Evol.* 57: 1149-1161.
- HUANG, S.S.-F., S.-Y. HWANG & T.-P. LIN, 2002. Spatial pattern of chloroplast DNA variation of *Cyclobalanopsis glauca* in Taiwan and East Asia. *Mol. Ecol.* 11: 2349-2358.
- HUDSON, R.R., M. SLATKIN & W.P. MADDISON, 1992. Estimation of levels of gene flow from DNA sequence data. *Genetics* 132: 583-589.
- IBRAHIM, K.M., R.A. NICHOLS & G.M. HEWITT, 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. *Heredity* 77: 282-291.
- JANG-LIAW, N.-H., T.-H. LEE & W.-H. CHOU, 2008. Phylogeography of *Sylvirana latouchii* (Anura, Ranidae) in Taiwan. *Zool. Sci.* 25: 68-79.
- JOHANSSON, F., 2003. Latitudinal shifts in body size of *Enallagma cyathigerum* (Odonata). *J. Biogeogr.* 30: 29-34.
- LIEFTINCK, M.A., J.-C. LIEN & T.-C. MAA, 1984. *Catalogue of Taiwanese dragonflies (Insecta: Odonata)*. Asian Ecol. Soc. Taichung.
- McLACHLAN, R., 1870. Descriptions of a new genus and four new species of Calopterygidae, and of a new genus and species of Gomphidae. *Trans. R. ent. Soc. Lond.* 18: 165-172.
- MILA, B., J.E. McCORMACK, G. CASTANEDA, R.K. WAYNE & T.B. SMITH, 2007. Recent postglacial range expansion drives the rapid diversification of a songbird lineage in the genus *Junco*. *Proc. R. Soc. (B)* 274: 2653-2660.
- MISOF, B., C.L. ANDERSON & H. HADRY, 2000. A phylogeny of the damselfly genus *Calopteryx* (Odonata) using mitochondrial 16S rDNA markers. *Mol. Phylog. Evol.* 15: 5-14.
- MULLEN, S.P. & J.A. ANDRES, 2007. Rapid evolution of sexual signals in sympatric *Calopteryx* damselflies: reinforcement or 'noisy-neighbour' ecological character displacement? *J. evol. Biol.* 20: 1637-1648.
- NICHOLAS, K.B., H.B. NICHOLAS, Jr & D.W. DEERFIELD, II, 1997. GeneDoc: analysis and visualization of genetic variation. *Embnew News* 4: 14.
- NICHOLS, R.A. & G.M. HEWITT, 1994. The genetic consequences of long distance dispersal during colonization. *Heredity* 72: 312-317.
- NYLANDER, J.A.A., 2004. *MrModeltest v2*. Program distributed by the author. Evolutionary Biology Centre, Uppsala Univ., Uppsala.
- ROZAS, J., J.C. SANCHEZ-DELBARRIO, X. MESSEGUER & R. ROZAS, 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics* 19: 2496-2497.
- SADEGHI, S., D. ADRIAENS & H. J. DUMONT, 2009. Geometric morphometric analysis of wing shape variation in ten European populations of *Calopteryx splendens* (Harris, 1782) (Zygoptera: Calopterygidae). *Odonatologica* 38: 341-357.
- SADEGHI, S., T. KYNDT & H.J. DUMONT, 2010. Genetic diversity, population structure and taxonomy of *Calopteryx splendens* (Odonata: Calopterygidae): an AFLP analysis. *Eur. J. Ent.* 107: 137-146.
- SEUTIN, G., L. M. RATCLIFFE & P. T. BOAG, 1995. Mitochondrial DNA homogeneity in the phenotypically diverse redpoll finch complex (Aves: Carduelinae: *Carduelis flammea-hornemanni*). *Evolution* 49: 962-973.
- SHIH, H.-T., H.-C. HUNG, C.D. SCHUBART, C.A. CHEN & H.-W. CHANG, 2006. Intraspecific genetic diversity of the endemic freshwater crab *Candidiopotamon rathbunae* (Decapoda, Brachyura, Potamidae) reflects five million years of the geological history of Taiwan. *J. Biogeogr.* 33: 980-989.

- SIMON, C., F. FRATI, A. BECKENBACH, B. CRESPI, H. LIU & P. FLOOK, 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Ann. Ent. Soc. Am.* 87: 651-701.
- SVENSSON, E.I., L. KRISTOFFERSEN, K. OSKARSSON & S. BENSCH, 2004. Molecular population divergence and sexual selection on morphology in the banded demoiselle (*Calopteryx splendens*). *Heredity* 93: 423-433.
- SWOFFORD, D. L., 2002. *PAUP*: phylogenetic analysis using parsimony (* and other methods)*. Sinauer Associates, Sunderland, Massachusetts.
- THOMPSON, J.D., T.J. GIBSON, T. PLEWNIAK, F. JEANMOUGIN & D.G. HIGGINS, 1997. The CLUSTALX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucl. Acids Res.* 25: 4876-4882.
- TODA, M., M. NISHIDA, M. MATSUI, K.-Y. LUE & H. OTA, 1998. Genetic variation in the Indian rice frog, *Rana limnocharis* (Amphibia: Anura), in Taiwan, as revealed by allozyme data. *Herpetologica* 54: 73-82.
- WEEKERS, P.H.H., J.F. DE JONCKHEERE & H.J. DUMONT, 2001. Phylogenetic relationships inferred from ribosomal ITS sequences and biogeographic patterns in representatives of the genus *Calopteryx* (Insecta: Odonata) of the West Mediterranean and adjacent West European zone. *Mol. Phylog. Evol.* 20: 89-99.
- WILLIAMSON, E.B., 1904. A new species of *Psolodesmus* (order Odonata) from Formosa. *Ent. News* 15: 247-250.
- YEH, W.-B., Y.-L. CHANG, C.-H. LIN, F.-S. WU & J.-T. YANG, 2004. Genetic differentiation of *Loxoblemmus appendicularis* complex (Orthoptera: Gryllidae): speciation through vicariant and glaciation events. *Ann. ent. Soc. Am.* 97: 613-623.

**WING SHAPE VARIATION IN
CALOPTERYX SPLENDENS (HARRIS) POPULATIONS
IN THE ZAGROS MOUNTAINS, IRAN
(ZYGOPTERA: CALOPTERYGIDAE)**

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C. splendens is found in most of Europe, large parts of Siberia and much of west and central Asia. There is great variation among ♂♂ in wing coloration. Traditionally, subspecific taxa have been distinguished by the size and position of the pigmented wing spot and by mating behaviour. About a dozen subspecies have been recognized, all of which are more or less geographically confined, but often with overlapping ranges and strong variation in wing spot size. Here, a geometric morphometrics is used to quantify morphological data and analyze the wing shape independent of wing spot size in 6 Zagros mountain populations, traditionally known as *C. s. intermedia*, based on wing spot size. 19 different points were digitized as landmarks on the left forewings of ♂♂, using GPA (Generalized Procrustes Analysis). The results reveal significant wing shape differences between all populations except Markazi and Lorestan on the one hand and Fasa and Kazeroon on the other hand. These observations confirm the role of geographic (here Dena, Oshtoran Kooh and Zard Kooh mountains of more than 4000 m altitude) and climatic barriers in population isolation, but also suggest that wing spot similarity does not necessarily reflect the full genetic similarity and evolutionary grouping of populations. Based on the wing shape analyzed, *C. splendens* is split into 2 distinguishable population groups in central and southern Zagros with 2 different gene pools, even though they show the same wing spot size, i.e., a long-term isolation among the groups investigated has occurred and the wing spot is not an infallible character for identifying *C. splendens* spp.

INTRODUCTION

Calopteryx splendens is a common zygopteran in Eurasia. It is a colourful species with a distinct courtship display in which colouration plays an important

part. The wings include a large number of veins, characteristic of the calopterygid family. They fly slowly and are restricted to clean running water (ASKEW, 2004; STETTNER, 1996).

The wing pigmentation in males is varied (SIVA-JOTHY, 1999) and a large number of subspecific taxa traditionally have been named based on the size and density of this wing spot (see SADEGHI et al., 2009) and on behaviour (MERTENS et al., 1992; DUMONT et al., 2005) because wing pigmentation correlates with reproductive isolation (GREYER, 1996; TYNKKYNEN, 2004). No morphological features corroborate these subspecies.

In Iran there are two subspecies, *C. s. orientalis* with a small apical wing spot, restricted to northern Iran, and *C. s. intermedia* with a large wing spot elsewhere in the country. The wing pigmentation is used for signaling in courtship (WAAGE, 1975). It seems that fitness is affected by flight performance (SPEIGHT et al., 2008). Different morphs may be the result of genetic adaptation and divergence or of phenotypic plasticity due to varying environments during evolutionary time (MERCKX & VAN DYCK, 2006).

Predation, courtship, finding oviposition sites, avoiding predators and other behavioural activities in winged insects are often dependent on an efficient and precise ability to fly (BREUKER et al., 2010). These behavioural activities are therefore expected to be under selection pressure. Studying such adaptations is important to understand how natural selection has shaped trait values. The shape of wings can be a good predictor of adaptation to different selection pressures (JOHANSSON et al., 2009). Wing shape can help to characterize populations within a species (HASS & TOLLEY, 1998; ROGGERO & d'ENTREVES, 2005; HOFFMAN & SHIRRIFS, 2002) and is useful to study complexes of species (DE LA RIVA et al., 2001) and/or the effects of hybridization (SMITH et al., 1997).

Traditional morphometrics are based on the application of standard multivariate analyses of collections of distance measures, ratios and angles, and typically represent only part of the information that may be obtained from the relative position of the landmarks on which these measurements are based. Geometric morphometrics is a technique that can answer questions about shape (geometric information of an object after removing location, orientation and scale) of the phenotype (BOOKSTEIN et al., 1991; ZELDITCH et al., 2004; DRYDEN & MARDIA, 1998). Geometric morphometrics is particularly appropriate to test quantitative representation of the phenotype that captures functional, genetic or developmental attributes (LAWING & POLLY, 2010). Insect wings have been studied by this method to illustrate relationships between populations (FRANCOY et al., 2009; SADEGHI et al., 2009), species (HASS & TOLLEY, 1998; MATIAS et al., 2001; HASSAL et al., 2007; HERNANDEZ et al., 2010; BENITEZ et al., 2011) and even higher taxa (GULER et al., 2006; JOHANSSON et al., 2009). Dragonfly wings also have been used in geometric morphometric studies

because wing veins play a key role in understanding the developmental processes underlying wing shape and its evolution.

The Zagros mountains, the largest mountain range in Iran, extend for approximately 1500 km from northwestern Iran to the Straits of Hormuz. They formed as a result of the collision between Arabia and Eurasia by an orogenic uplift during the Cenozoic (MOLNAR, 2006). Many peaks are over 3,000 and some over 4,000 m (MARKER & HEYDARI-GURAN, 2009). The winters are severe, with temperature often below -25°C . Summer and autumn are dry (FREY & PROBST, 1986). The Zagros mountains generally divide the Mediterranean climatic zone (to the west of the mountains) from the arid-West Asian zone. They have a Mediterranean climate and can be divided into regional climatic zones, depending on altitude and longitude, which show distinct vegetation types (BOBEK, 1968). Such mountain ranges may be important barriers, particularly if they simultaneously separate climatic zones. As mountains are efficient barriers for lowland animals, so are valleys for mountain species (MAYR, 1963). Some rivers and springs are inhabited by Odonata such as *Calopteryx splendens*.

In this study we investigated wing shape differences between six populations of *C. splendens* on the flanks of the Zagros mountains. We expected to find variation due to geographic and topographic differences.

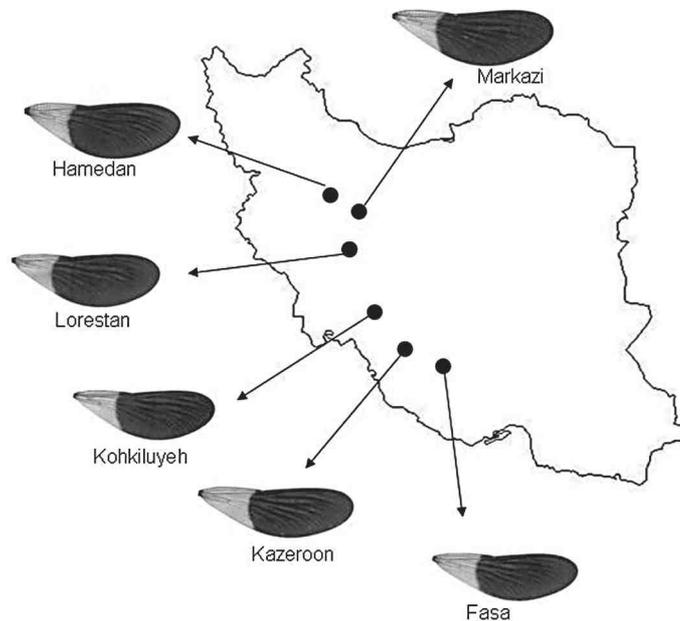


Fig. 1. Localities and left forewing as a symbol for each population.

MATERIAL AND METHODS

A total number of 158 *Calopteryx splendens* specimens was collected from six sites in Zagros (Fig. 1), viz. Kazeroon (29:37 N, 51:36 E), Fasa (28:43 N, 52:37 E), Hamedan (35:05 N, 48:37 E), Kohki-luyeh (30:43 N, 50:31 E), Lorestan (33:35 N, 50:04 E), Markazi (34:06 N, 49:19 E).

All specimens, fixed in ethyl alcohol 70%, were dried for about one hour before scanning. The left forewings were scanned using a flatbed scanner (Agfa SNAPSCAN 1236) with a white background illumination as a color image at 500 dpi resolution. The wings were not cut off and 2D images were captured using a white piece of plastic and a small transparent card. We digitized 18 landmarks per wing of all specimens that possessed at least one intact forewing using tpsDig 2.16 (ROHLF, 2010, available from <http://life.bio.sunysb.edu/morph/>). These landmarks were chosen at the intersection of veins in the hyaline part of the wing for their ability to represent the shape and major dimensions of the wing (BOOKSTEIN, 1991). All landmarks are shown in Figure 2.

To ensure that shape variation was adequately represented after projection in the tangent space, we calculated the correlation between the procrustes and tangent shape distances using tpsSmall software (ROHLF, 2003). Digitization error due to finding the same landmark place in different samples is important when analyzing wing shapes. To assess this error we used the protocol by ADRIAENS, available from <http://www.fun-morph.ugent.be/miscel/methodology/morphometrics.pdf>. Analysis of shape variation was performed using geometric morphometrics (ROHLF & MARCUS, 1993, ADAMS et al., 2004). A Generalized Procrustes Analysis (GPA) algorithm was applied to superimpose landmark configurations using PAST (HAMMER & HARPER, 2001). In this procedure the variation due to differences in size, location and rotation of samples is removed but shape is preserved (SLICE, 2001; ROHLF, 1999). Centroid size, square root of summed square distances from each landmark to the configuration mean point (BOOKSTEIN, 1991; SLICE & BOOKSTEIN, 2007), was used as a measure of overall size variation of wings. A one way ANOVA (Analysis of Variance) for whole data and F and T test for two samples were conducted using PAST to show significant differences of centroid size between and within populations and to define pair-wise differences in centroid size respectively.

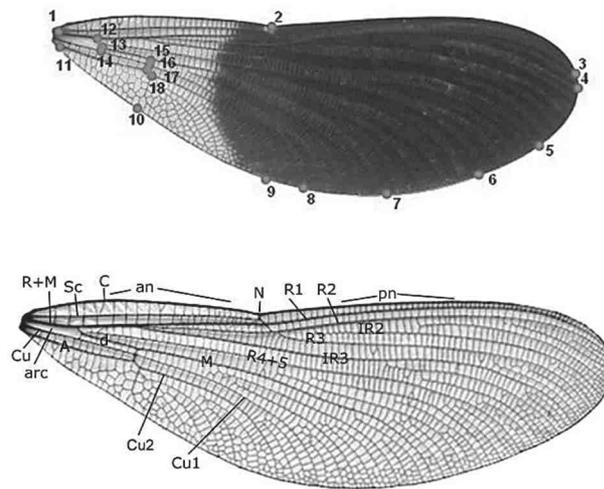


Fig. 2. Landmark positions on the wing and wing venation in *Calopteryx splendens*.

Once shape coordinates, which are a reduced number of variables that collectively describe the variation in the original shapes, have been derived using one of these methods, any type of multivariate statistical analysis can be performed (DRYDEN & MARDIA, 1998; ZELDITCH et al., 2004).

The most common and simple methods for ordinating specimens, principal components analysis (PCA), was carried out to ordinate specimens along the major axis of shape variation. Multivariate analysis of variance (MANOVA) and two group

permutation tests with 2000 permutations were performed to show overall shape differences between groups and Hotelling's T²-test were conducted as pair-wise comparisons to analyze differences in mean shape between groups using IMP (SHEETS, 2000), available at <http://www3.canisius.edu/~sheets/moremorph.html>. Canonical variate analysis (CVA), a common analysis for finding the features that best differentiate between known groups, was also used and the differentiation between groups illustrated as a CVA scatterplot.

Thin-plate spline analysis based on tangent space projections was conducted (BOOKSTEIN, 1991; ZELDITCH et al., 2004). For each population the mean configurations were illustrated based on deformation grids using tpsSpln (ROHLF, 2004) to visualize differences in position of individual landmarks between one wing shape and another as a graphic deformation. In this manner, a consensus of wing coordinates were used as a reference and a consensus of wing coordinates of each population were used as data in the software. Relative warp ordination plot was also illustrated using consensus data in tpsRelw 1.46 (ROHLF, 2008). A matrix of procrustes distances as a pair-wise population consensus configuration was used to illustrate phenetic relationships between populations in a phenogram derived by UPGMA (Unweighted Pair-Group Method with Arithmetic means), a hierarchical clustering method with the most cophenetic correlations to the original procrustes distance matrix, using NTSYSpc (ROHLF, 2002).

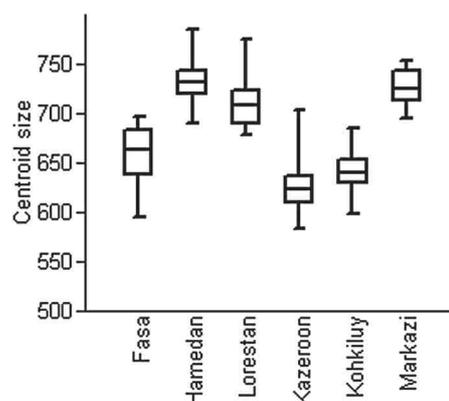


Fig. 3. Mean centroid size of the six Zagros mountain *Calopteryx splendens* populations.

RESULTS

Centroid size as a criterion of wing size was calculated for all wings (Fig. 3). Maximum and minimum centroid sizes were in Hamedan and Kazeroon, respectively. Furthermore, populations from Hamedan, Markazi and Lorestan in central Zagros had larger mean sizes than three populations from the southern part of the mountains. A one-way ANOVA showed significant centroid size differences between and within populations ($F = 104.8$, $p = 0.000$). Tukey's HSD test which compares pair-wise, did not show significant differences ($p > 0.05$) in wing size between Kohkiluyeh & Fasa, Hamedan & Markazi and Markazi & Lorestan; the population of Kazeroon had the smallest wing size which was followed by Kohkiluyeh and Fasa. Hamedan, Markazi and Lorestan populations had the largest wing sizes.

The results of PCA, like the relative warp analysis, explained more than 70% of shape variation in the first three PCs resulting from the variance-covariance matrix (PC1, 38.24%; PC2, 18.88% and PC3, 13.92%). Up to seven axes are needed to cover more than 90% of the shape variation. A PC1 vs PC2 scatter plot uncovered the relationship between the three central populations of Zagros and the other three populations in the southern part of the Mountains (Fig. 4). A small

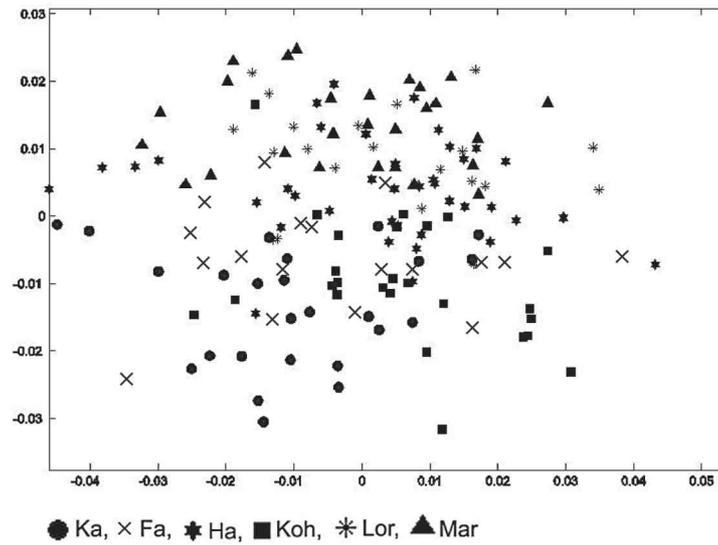


Fig. 4. PC1 vs PC2 screen plot. — Ka: Kazeroon; — Fa: Fasa; — Ha: Hamedan; — Koh: Kohkiluyeh; — Lor: Lorestan; — Mar: Markazi.

overlap is shown between these two groups.

An overall mean wing shape for the six populations calculated by GPA analysis using least-squares superimposition and analyzed using MANOVA showed that wing shape differences between populations were significant (*Wilk's lambda* = 0.017, $p = 0.000$, $F = 4.86$). Hotelling's pair-wise comparison as a *post-hoc* F-test with 900 bootstraps indicated significant differences ($p < 0.01$) between all populations except Kazeroon & Fasa in the south and Markazi & Lorestan in

Table I

Hotelling's pair wise comparisons and Bootstrapped F-test (with 900 bootstraps) and related p values for the Zagros mountains' populations on upper right and lower left diagonal respectively

Population	Kazeroon	Fasa	Hamedan	Kohkiluyeh	Lorestan	Markazi
Kazeroon	-	3.03	12.06**	6.57**	22.15**	11.98**
Fasa	2.56	-	8.82**	3.26*	9.04*	11.01**
Hamedan	12.56**	4.58**	-	15.51**	6.07**	5.25**
Kohkiluyeh	7.05**	2.16*	6.94**	-	10.63**	12.69**
Lorestan	11.49**	4.25**	2.82*	7.14**	-	2.17
Markazi	16.64**	7.27**	5.06**	14.86**	1.60	-

* < 0.05

** < 0.01

central part of the mountains (Tab. I). CVA showed differences between all populations but some overlap between Kazeroon and Fasa and between Markazi and Lorestan was visible (Fig. 5).

A relative warp ordination plot revealed differences between central Zagros (Hamedan, Lorestan and Markazi) and the three southern Zagros populations (Kohkiluyeh, Kazeroon and Fasa). In addition, thin-plate spline deformation grids showed causes of the shape differences visually (Fig. 6).

The phenogram obtained by UPGMA clustering indicated relationships among populations and supported the results of the relative warp analysis demonstrated as ordination plot as well (Figs 6, 7).

DISCUSSION

Calopteryx splendens subspecies are often confusing (DUMONT, 1972). Based only on wing pigmentation, wing spot size may overlap and some forms may lack pigmentation completely. In Iran, *C. s. orientalis*, restricted to the coastal margin of Caspian Sea, has a small apical wing spot; *C. s. intermedia* in other parts of the country including the Zagros mountains has a large wing spot, from the nodal part of the wing or more proximal to the tip. SADEGHI (2008) indicated two separate populations in Zagros based on ten traditional morphomet-

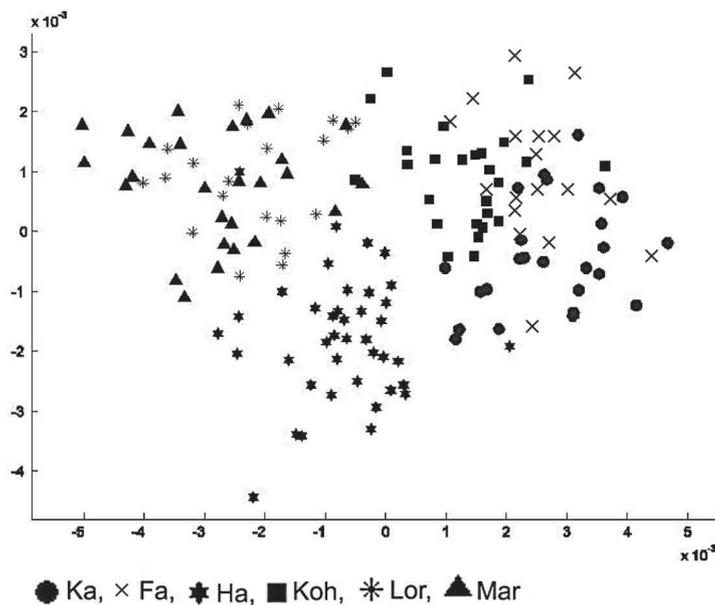


Fig. 5. CV1 vs CV2. Ka, Kazeroon; Fa, Fasa; Ha, Hamedan; Koh, Kohkiluyeh; Lor, Lorestan; Mar, Makazi

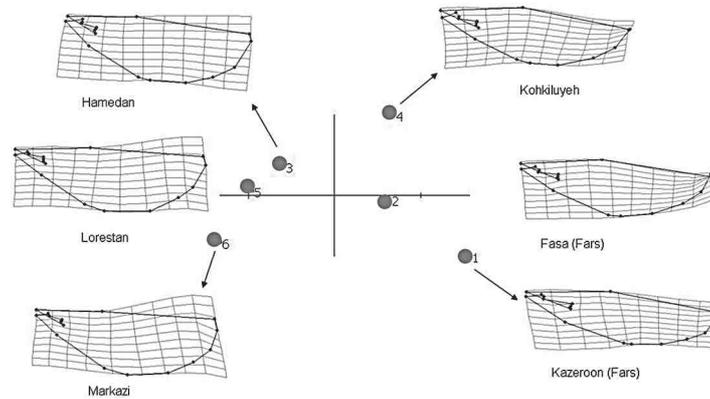


Fig. 6. Relative warp ordination plot of consensus data of the Zagros mountains' populations and related Thin-plate grids

ric wing characters, but in relation to other populations, these results were not sufficiently reliable. Considerable inter-population differences in wing size were found between two populations groups, and the southern population of Zagros had smaller wings than the central populations.

Data analysis using GM technique revealed shape differentiation between all populations in the Zagros Mountains except the pair Lorestan - Markazi ($p < 0.01$) in the central part and Kazeroon - Fasa ($p < 0.05$) in the south. These results suggest two distinct gene pools in Zagros.

Topography is the most important factor affecting wing shape. Mountains provide isolated habitats with limited possibility of dispersal between them. The presence of high altitudes, such as Zardkooh, Oshtorankoo and Dena at more than 4000 meters height, clearly plays the role of a geographic barrier, which, along with limited dispersal capabilities of *Calopteryx*, leads to diversification of the taxon. The differentiation of these populations is assumed to have occurred through natural selection acting upon geographically isolated gene pools.

Moreover, there is a climatic difference between central and southern Zagros. The central part that includes Lorestan, Markazi and Hamedan is Mediterranean and the southern part including Kazeroon, Fasa and Kohkiluyeh has a semi-continental climate. These differences can affect daily activity periods of the insects. Therefore, a climatic barrier is a second factor preventing populations of central and southern parts from merging.

Based on wing shape and size, the status of the groups from central and southern Zagros is one of evolutionarily independence: *C. splendens* in two separate parts of the Zagros mountains has developed very different wing shapes and sizes. Wing shape differences were associated with displacement of outer landmarks in males (landmarks 3-9) that are located at the distal and ventral parts of the wing.

All landmarks however reflect wing length and width.

Wing shape variation revealed phenotypic differentiation among *Calopteryx* in the central and southern parts but not among all populations. Such subtle wing morphometric distinctiveness among populations was also found in other damselfly species (HASSAL et al., 2007). Based on the shape analyzed, *C. splendens* is split into two clearly differentiated groups in the Zagros mountains. This suggests a long-term isolation among the groups investigated, which is assumed to have occurred as a result of genetic drift and natural selection acting upon geographically isolated and originally very small random samples of the gene pools concerned.

Climatic differences and wing shape differentiation between *C. splendens* population groups between the two parts of the Zagros strongly suggest that gene arrangement has changed and correlated change in wing shape has occurred as a response to thermal differences in central and southern Zagros. Such genetic changes in wing shape have been confirmed in *Drosophila subobscura* because of gene-inversion linkage disequilibria by SANTOS et al. (2004). Moreover, some behaviour such as mating and foraging may also differ between two geographical separated populations and such differences could affect wing shape.

The consistency of this pattern of inter-population variation is also evident in other *Calopteryx* populations in Europe (SADEGHI et al., 2009). Therefore, associated with previous findings, the current study has located the wing region as of taxonomic importance, even if perhaps not at the subspecies level. The occurrence of similar patterns of wing spot in different populations of *Calopteryx* might reflect conservative genetic constraints, but only further analysis will offer a precise explanation.

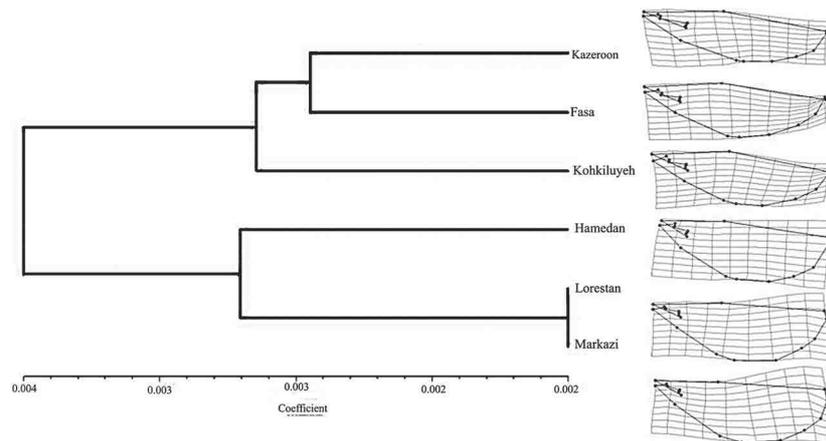


Fig. 7. UPGMA phenogram of six populations from the Zagros mountains and related Thin-plate deformation grids

REFERENCES

- ADAMS, D.C., F.J. ROHLF & D. SLICE, 2004. Geometric morphometrics: ten years of progress following the 'revolution'. *Ital. J. Zool.* 71: 5-16.
- ADRIAENS, D., 2007. <http://www.fun-rph.ugent.be/Research/Methodology/Morphometrics.pdf>
- ASKEW, R.R., 2004. *The dragonflies of Europe*. [Revised edn]. Midas Printing, China.
- BENITEZ, H.A., L.E., PARRA, E., SEPULVEDA & M.J. SANZANA, 2011. Geometric perspectives of sexual dimorphism in wing shape of Lepidoptera: the case of *Synneuria* sp. (Lepidoptera: Geometridae). *J. Ent. Res. Soc.* 13: 53-60
- BOBEK, H., 1968. Vegetation, In: W.B. Fisher, [Ed.], *The Cambridge history of Iran*, Vol. 1: *The land of Iran*, pp. 28-293, Cambridge Univ. Press, Cambridge.
- BOOKSTEIN, F.L., 1991. *Morphometric tools for landmark data: geometry and biology*. Cambridge Univ. Press, Cambridge.
- BREUKER C. J., M. GIBBS, S. VANDONGEN, T. MERCKX & H. VAN DYCK, 2010. The use of geometric morphometrics in studying butterfly wings in an evolutionary ecological context. In: A.M.T. Elewa, [Ed.], *Morphometrics for nonmorphometricians*, Lecture notes in Earth Sciences 124, DOI 10.1007/978-3-540-95853-6_12, C_ Springer-Verlag Berlin Heidelberg 2010.
- DE LA RIVA, J., F. LE PONT, V. ALI, A. MATIAS, S. MOLLINEDO & J.P. DUJARDIN, 2001. Wing geometry as a tool for studying the *Lutzomyia longipalpis* (Diptera: Psychodidae) complex. *Mems Inst. Oswaldo Cruz* 96: 1089-1094.
- DRYDEN, I.L. & K.V. MARDIA, 1998. *Statistical shape analysis*. John Wiley & Sons.
- DUMONT, H.J., 1972. The taxonomic status of *Calopteryx xanthostoma* (Charpentier, 1825) (Zygoptera: Calopterygidae). *Odonatologica* 1: 21-29.
- DUMONT, H.J., 1991. *Odonata of the Levant*. [Fauna Palestina, Vol. 5]. Israel Acad. Sci. & Humanities, Jerusalem.
- DUMONT, H.J., H. HEIDARI & K.I. ATAMURADOV, 1997. Hybridisation in *Calopteryx orientalis* (Selys) East of the shores of the south Caspian lake (Zygoptera: Calopterygidae). *Odonatologica* 26: 205-213.
- DUMONT, H.J., P.H.H. WEEKERS, J.R. VANFLETEREN & J.DE JONCKHEERE, 2005. Phylogenetic relationships, divergence time estimation and global biogeographic patterns of calopterygoid damselflies (Odonata, Zygoptera) inferred from ribosomal DNA sequences. *Syst. Biol.* 54: 347-362.
- FRANCOY, T.M., D. WITTEMANN, V. STEINHAGE, M. DRAUSCHKE, S. MULLER, D.R. CUNHA, A.M. NASCIMENTO, V.L.C. FIGUEIREDO, Z.L.P. SIMOES, D. De JONG, M.C. ARIAS & L.S. GONÇALVES, 2009. Morphometric and genetic changes in a population of *Apis mellifera* after 34 years of Africanization. *Genet. mol. Res.* 8(2): 709-711.
- FREY, W. & W. PROBST, 1986. A synopsis of the vegetation in Iran. In: H. Kurschner, [Ed.], *Contribution to the vegetation of Southwest Asia*, pp. 9-43. Wiesbaden.
- GRETHER, G.F., 1996. Sexual selection and survival selection on wing coloration and body size in the rubyspot damselfly *Hetaerina americana*. *Evolution* 50: 1939-1948.
- GULER et al., 2006. Systematical studies on Anthidiini (Hymenoptera: Megachilidae): a geometric morphometrics approach. *Acta ent. sin.* 49(3): 474-483.
- HAAS, H.L. & K.A. TOLLEY, 1998. Geographic variation of wing morphology in three Eurasian populations of the fruit fly *Drosophila lummei*. *J. Zool. Lond.* 245: 197-203.
- HAMMER, Øy. & D.A.T. HARPER, 2007. *PAST – Paleontological Statistics*, version 1.62. (<http://folk.uio.no/ohammer/past>).
- HASSAL, C., D.J. THOMPSON & I.F. HARVEY, 2008. Wings of *Coenagrion puella* vary in shape at the northern range margin (Odonata: Coenagrionidae). *Int. J. Odonatol.* 11: 35-41.
- HERNANDEZ-L., N., A.R. BARRAGAN, S. DUPAS, G.F. SILVAIN & O. DANGLES, 2010. Wing shape variations in an invasive moth are related to sexual dimorphism and altitude.

- Bull. ent. Res.* 100: 529-541.
- HOFFMAN, A.A. & J. SHIRRIFS, 2002. Geographic variation for wing shape in *Drosophila serrata*. *Evolution* 56: 1068-1073.
- JOHANSSON, F., M.S. DERQUEST & F. BOKMA, 2009. Insect wing shape evolution: independent effects of migratory and mate guarding flight on dragonfly wings. *Biol. J. Linn. Soc.* 97: 362-372.
- LAWING, A.M. & P.D. POLLY, 2010. Geometric morphometrics: recent applications to the study of evolution and development. *J. Zool.* 280: 1-7.
- MARKER M. & S. HEYDARI-GURAN, 2009. *Application of data-mining technologies to predict Paleolithic site locations in the Zagros mountains of Iran*. Computer applications to archaeology, Williamsburg/VA.
- MATIAS, A., J.X. DE LA RIVA, M. TORREZ, J.P. DUJARDIN, 2001. *Rhodnius robustus* in Bolivia identified by its wings. *Mems Inst. Oswaldo Cruz* 96(7): 947-950.
- MAYR, E., 1963. *Animal species and evolution*. Harvard Univ. Press, Cambridge/ MA.
- MERCKX, T. & H. VAN DYCK, 2006. Landscape structure and phenotypic plasticity in flight morphology in the butterfly *Pararge aegeria*. *Oikos* 113: 226-232.
- MERTENS, J., W. DE COSTER, H. DE MAYER & H.J. DUMONT, 1992. A method for the quantitative analysis of wing spots applied to two populations of *Calopteryx splendens* (Harris) (Zygoptera: Calopterygidae). *Odonatologica* 21: 443-451.
- MOLNAR, M., 2006. *Tertiary development of the Zagros mountains*. Available in: http://www.uwec.edu/jolhm/Student_Research/Molnar/reports/zagros.pdf
- ROGGERO, A. & P.P. d'ENTREVES, 2005. Geometric morphometric analysis of wing variation between two populations of the *Scythris obscurella* species-group: geographic or interspecific differences? (Lepidoptera: Scythrididae). *Shilap Revta Lepid.* 33: 101-112.
- ROHLF, F.J., 1999. Shape statistics: Procrustes superimpositions and tangent spaces. *J. Classificat.* 6: 197-223.
- ROHLF, F.J., 2002. *NTSYSpc numerical taxonomy and multivariate analysis system, version 2.11 user guide*. Dept Ecol. & Evol., St. Univ. New York, Stony Brook, New York.
- ROHLF, F.J., 2003. *tpsSmall, version 1.20 ed*. Dept Ecol. & Evol., St. Univ. New York, Stony Brook, New York.
- ROHLF, F.J., 2004. *Thin-plate spline, digitize landmarks and outlines, version 1.20*. Dept Ecol. & Evol., St. Univ. New York, Stony Brook, New York.
- ROHLF, F.J., 2008. *tpsRelw, relative warps analysis, version 5/13/05*. Dept Ecol. & Evol., St. Univ. New York, Stony Brook, New York.
- ROHLF, F.J., 2010. *tpsDig2, digitize landmarks and outlines, version 2.10*. Dept Ecol. & Evol., St. Univ. New York, Stony Brook, New York.
- ROHLF, F.J. & L.F. MARCUS, 1993. A revolution in morphometrics. *Trends Ecol. Evol.* 8: 129-132.
- SADEGHI, S., 2008. *Aspects of infraspecific phylogeography of Calopteryx splendens (Calopterygidae, Odonata)*. PhD Thesis, Gent Univ.
- SADEGHI, S., D. ADRIAENS, H.J. DUMONT, 2009. Geometric morphometric analysis of wing shape variation in ten European populations of *Calopteryx splendens* Harris (1782) (Zygoptera: Odonata). *Odonatologica* 38(4): 343-360.
- SANTOS, M., P.F. IRIARTE, W. CESPEDES, J. BALANYA, A. FONTDEVILA & L. SERRA, 2004. Swift laboratory thermal evolution of wing shape (but not size) in *Drosophila subobscura* and its relationship with chromosomal inversion polymorphism. *J. evol. Biol.* 17: 841-855.
- SHEETS, H.D., 2000. *Integrated Morphometrics Package (IMP)*. Available at <http://www3.canisius.edu/~sheets/moremorph.html>
- SIVA-JOTHY, M.T., 1999. Male wing pigmentation may affect reproductive success via female choice in a calopterygid damselfly (Zygoptera). *Behaviour* 136: 1365-1377.
- SLICE, D.E., 2001. Landmark coordinates aligned by Procrustes analysis do not lie in Kendall's

- shape space. *Syst. Biol.* 50:141-149.
- SLICE, D.E. & F.L. BOOKSTEIN, 2007. A glossary for geometric morphometrics. Online, <http://life.bio.sunysb.edu/morph/glossary/gloss1.html>
- SMITH, D.R., B.J. CRESPI & F.L. BOOKSTEIN, 1997. Fluctuating asymmetry in the honey bee, *Apis mellifera*, effects of ploidy and hybridization. *J. evol. Biol.* 10: 551-574.
- SPEIGHT, M.R., M.D. HUNTER & A.D. WATT, 2008. *Ecology of insects: concepts and applications*. Wiley-Blackwell, Oxford.
- STETTNER, C., 1996. Colonisation and dispersal patterns of banded (*Calopteryx splendens*) and beautiful demoiselles (*C. virgo*) (Odonata: Calopterygidae) in south-east German streams. *Eur. J. Ent.* 93: 579-593
- TYNKKYNEN, K., M.J. RANTALA & J. SUHONEN, 2004. Interspecific aggression and character displacement in the damselfly *Calopteryx splendens*. *J. evol. Biol.* 17: 259-267.
- WAAGE, J.K., 1975. Reproductive isolation and the potential for character displacement in the damselflies *Calopteryx maculata* and *C. aequabilis* (Odonata: Calopterygidae). *Syst. Zool.* 24(1): 24-36.
- ZELDITCH, M.L., D.L. SWIDERISKI, H.D. SHEETS & W.L. FINK, 2004. *Geometric morphometrics for biologists: a primer*. Elsevier Acad. Press, London.

MORPHOFUNCTIONAL GROUPS OF ODONATA LARVAE IN THREE FRESHWATER ECOSYSTEMS FROM EASTERN CUBA

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Five morphofunctional groups were determined, based on the morphological characters of the exuviae and the behaviour of the larvae, in three freshwater habitats from Santiago de Cuba. The exuviae were collected weekly over a year, within an 8 m transect and 1 m wide, in the water-ground transition, directly on vegetation, rocks or ground. The most diverse group was the lamellates with 12 spp., followed by the epibenthonics with 11; the least diverse was the hidden group which included the only 2 Gomphidae known from Cuba, together with *Cannaphila insularis funerea* and *Orthemis ferruginea*, all gallery diggers. The Zygoptera were represented by over 25% of the spp. observed in each habitat, whilst the Aeshnidae always had less than 10% of the individuals. The Libellulidae, the most diverse family within the Anisoptera, accounted for the greatest diversity among the morphofunctional groups.

INTRODUCTION

The larvae of odonates are generally aquatic, except for a few amphibious or terrestrial species (CORBET, 1999; WATSON, 1982). Their high morphological and ethological diversity is related to the variety of aquatic microhabitats and the interaction of biotic and abiotic variables (CORBET, 1962; PAULSON, 1982). The use of environment depends on the larval developmental stage, predating strategies, size of the prey, and refugia (CORBET, 1983; 1999). Although seasonal changes and nutritional habits contribute to niche segregation between the larvae, microhabitat is still considered the main cause (JOHNSON & CROWLEY, 1980).

The sprawlers are a group of semi-buried species in muddy bottoms of temporary lentic environments, in the almost complete absence of vegetation (WATSON,

1962). Most of them are considered thigmotactic, lying still, in the bottom, with legs extended as mechanoreceptors (ZAHNER, 1959; WATSON, 1962; PAULSON, 1982; WINSTANLEY, 1984).

On the other hand, the greatest diversity of odonates can be found in permanent or temporary lentic habitats with abundant vegetation (CORBET, 1999). Species in families such as Coenagrionidae, Lestidae, Aeshnidae and Libellulidae display mimetic colouring patterns related to their environment (CORBET, 1957). The limbs of these species are adapted for climbing or grasping the vegetation, and lateral rather than frontal eyes have evolved, thereby improving their all round vision (NEEDHAM & WESTFALL, 1955; NEEDHAM et al., 2000). TILLYARD (1917) recorded black larvae of *Rhadinosticta simplex* (Martin) in the bottom detritus and brown ones on emergent plants. The larvae of *Anax* are striped with brownish and lighter bands while living among the macrophytes near the surface (WESENBERG-LUND, 1913). He also noticed that the colouring patterns of *Aeshna grandis* (L.) larvae change between seasons, being green during the summer and brown in winter.

The claspers, species which grasp stones in rivers and streams, use their caudal gills and ventral setae to hold onto the surface (ASAHINA, 1950). Zygopterans such as *Cora* spp. are included in this group (CALVERT, 1911), together with some libellulids with a hairless hydrodynamic body that reduces drag. Other inhabitants of lotic bodies are the Gomphidae, whose larvae burrow in the bottom. These species have a long cylindrical body and the last abdominal segment is elongated to aid rectal breathing (CORBET, 1962).

Zygopteran larvae with small caudal gills inhabit motile and rapid waters (HIROSE & ROKUYAMA, 1963) while those inhabiting still waters, have leafy caudal gills and expanded distal parts of the body (RAMÍREZ, 1997). For example, the larvae of *Protoneura aurantiaca* Selys live in oxygen rich environments and have caudal gills that occupy 30% of the body length (NOVELO, 1994), whereas those of *Acanthagrion quadratum* Selys prefer still, oxygen poor waters in the dry season and their caudal gills account for nearly 80% of the body length (NOVELO, 2009). WILLIAMS (1936) affirmed that the area of the caudal gills in zygopterans is inversely proportional to oxygen availability in the water.

Once the larval cycle is concluded, the transition or metamorphosis of the last instar larva into the adult phase takes place through emergence. In order to emerge, the larva moves out of the water onto the vegetation, dry branches or rocks; and by a process involving hormonal changes exits from the exoskeleton (ESQUIVEL, 2006).

The exuviae that remain on the emergence substrate provide a potential source of indirect information about the natural history, conduct and ecology of aquatic insects (SOLUK, 1990). The exuviae of Odonata have been used to determine patterns of emergence during a year or within a season, sex ratio at emergence and the size and density of emergence (CORBET, 1999). Also, an exuvia is clear

evidence of the completion of the life cycle of that species and hence is proof of breeding at that site, and is indicative of the environmental quality of freshwater habitats (RAEBEL et al., 2010).

This study aims to determine groups of species of Odonata by using morphological and ethological characteristics of the larval phase, based on the collection of exuviae from three freshwater habitats in Santiago de Cuba, Cuba.

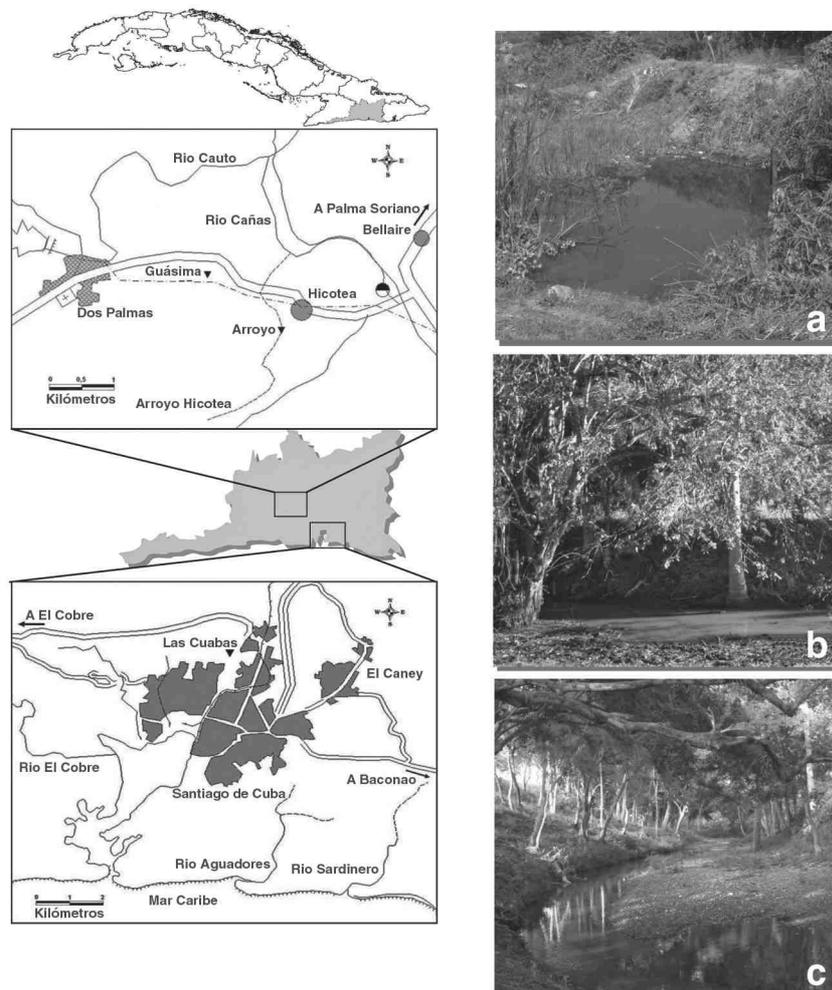


Fig. 1. Geographical locality of the three habitats: (a) permanent lentic; – (b) temporary lentic; – (c) lotic.

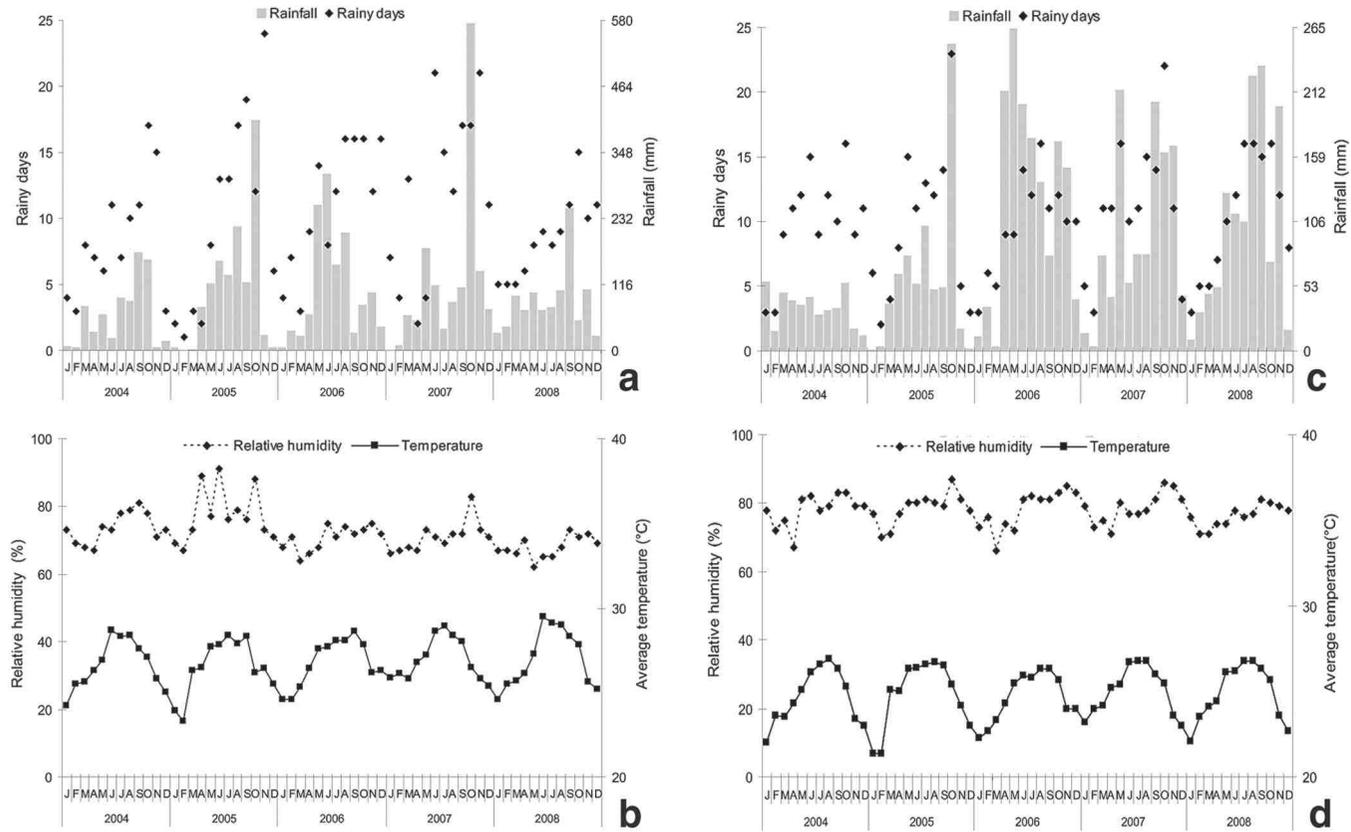


Fig. 2. Rainfall, rainy days, relative humidity and temperature registered monthly between 2004 and 2008: (a, b) permanent lentic; – (c, d) temporary lentic and lotic habitats. – Weather records were provided by the Centro Meteorológico Provincial de Santiago de Cuba, fit to the coordinates of each location.

MATERIAL AND METHODS

The study was conducted in three habitats: permanent lentic, with full insolation (Las Cuabas), temporary lentic (Guásima) and lotic (Arroyo), the last two with filtered insolation. Las Cuabas is a 120m² permanent pond located North on the Main Road, 5½km from the city (75°49'08" W and 20°03'32" N) (Fig. 1a). The bottom is muddy with stones and gravel and reaches a depth of 85cm. The vegetation is typically riparian (CAPOTE & BERAZAÍN, 1984), with abundant *Typha dominicensis* (Pers.) Kunth, *Eichhornia crassipes* (Mart.) Solms and *Cyperus involucratus* Rottb. Fish specimens of *Gambusia punctata* (Poey) around 4.5cm long were observed.

The annual historical rainfall fluctuates between 740-1,400mm, relative humidity varies from 71-77% and the average temperature is 26.5-26.9°C (22.1°C minimum, 32.5°C maximum) (Fig. 2a, b). Average wind speed is 8.2km/h.

Guasima (76°03'22" W and 20°06'44" N) and Arroyo (76°02'32" W and 20°07'42" N) are located in Dos Palmas, North Santiago de Cuba, in the municipality of Palma Soriano (Fig. 1b, c). The annual historical rainfall fluctuates between 714-1 150mm, average relative humidity varies between 77.8 and 86.7%, with an average annual temperature of 24.8°C (21.4°C minimum, 26.8°C maximum) (Fig. 2c, d). The wind speed was 2.4km/h.

Guasima is a 160m² temporary pond overshadowed by large trees, with dominant secondary grass-land vegetation (CAPOTE & BERAZAÍN, 1984) and isolated trees in the ecotope of a gallery forest (Fig. 1b). Herbs are represented by *Panicum* sp. and *Cyperus ochraceus* Vahl, 1805. The bottom reaches a depth of 45cm and is muddy with isolated stones and abundant dead leaves. This habitat was dry between February 29th and May 3rd, 2008.

Arroyo is a secondary forest (CAPOTE & BERAZAÍN, 1984) in a gallery forest ecotope (Fig. 1c), dominated by *Cecropia schreberiana* Miq. The aquatic vegetation consists mainly of Cyperaceae. The river bottom is sandy gravel, with an average depth of 50cm, and is dominated by *Cladophora* sp. during the non rainy season. The shores have scarce vegetation cover and the stream speed was 0.17 m/s. of the fish *Gambusia punctata*, *Micropterus salmoides* (Lacepède) and *Nandopsis tetracanthus* (Cuvier & Valenciennes) were observed.

Exuviae were collected in 42 surveys from August 2007 to July 2008 in Las Cuabas and between January and December, 2008 in Guasima and Arroyo. All exuviae were removed from the habitat prior to the surveys. Surveys started at 09.00 h (TROTIER, 1973; CORBET, 1999) and lasted for 5 h. The frequency varied between 7 and 9 days according to the protocol of JOHANSSON & BRODIN (2003), JOHANSSON et al. (2005) and based on previous observations of each habitat. Whenever rain was announced, the surveys were moved forward to reduce the loss of exuviae.

Samples were made along an 8m transect with a width of 1m. Exuviae were collected directly from the vegetation, land or rocks (JOHANSSON & BRODIN, 2003; JOHANSSON et al., 2005) and preserved in 25ml labeled bottles containing 70% alcohol. Species were identified under a Carl Zeiss stereoscopic microscope using the key to Cuban larval odonates by TRAPERRO & NARANJO (2009) and deposited in the Odonata Larvae Reference collection at the Universidad de Oriente. The total length of the exuviae was measured using a millimeter ocular lens.

A morphofunctional group is here defined as a set of species sharing a common set of morpho-

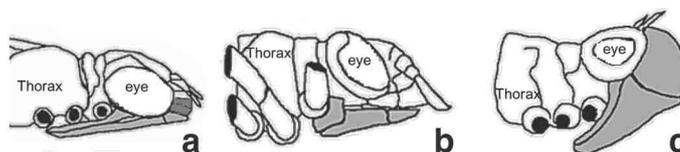


Fig. 3. Types of labium: (a) flat; – (b) flat; – (c) slightly concave. – The gray area represents the position of labium under the ventral-anterior surface of the head. [Modified from Misof, 2002].

Table I
Percentage of odonate exuviae collected on the habitats, permanent lentic (LP), temporary lentic (LT) and lotic (L)

Families	Species	Habitats		
		LP	LT	L
Lestidae	<i>Lestes forficula</i> Rambur, 1842		2.3	0.2
	<i>L. spumarius</i> Hagen in Selys, 1862		0.5	
	<i>L. tenuatus</i> (Rambur, 1842)		9.5	1.7
Protoneuridae	<i>Neoneura maria</i> (Scudder, 1866)*	0.2		9.9
	<i>Protoneura capillaris</i> (Rambur, 1842)*	0.2	1.4	17
Coenagrionidae	<i>Enallagma civile</i> (Hagen, 1861)	3.7		
	<i>E. coecum</i> (Hagen, 1861)	3.2	0.9	6.3
	<i>Ischnura capreolus</i> (Hagen, 1861)	0.2		
	<i>I. hastata</i> (Say, 1839)		2.8	0.5
	<i>I. ramburii</i> (Selys, 1850)	0.4		
	<i>Leptobasis vacillans</i> Hagen in Selys, 1877	0.9	0.2	
Aeshnidae	<i>Telebasis dominicanum</i> (Selys, 1857)**	10.4	0.5	0.2
	<i>Anax amazili</i> (Burmeister, 1839)		0.5	
	<i>A. junius</i> (Drury, 1770)	1.8		
	<i>Coryphaeschna adnexa</i> (Hagen, 1861)	8.1	0.2	
	<i>Gynacantha nervosa</i> Rambur, 1842		0.9	0.7
	<i>Rhionaeschna psilus</i> (Calvert, 1947)		3.5	1.6
	<i>Triacanthagyna septima</i> (Selys, 1857)		2.8	0.2
	<i>Aphylla caraiba</i> (Selys, 1854)	1.2		
Gomphidae	<i>Progomphus integer</i> Hagen in Selys, 1878**	0.4		5.8
	<i>Cannaphila insularis funerea</i> (Carpenter, 1897)	0.2		
Libellulidae	<i>Crocothemis servilia</i> (Drury, 1770)	14	2.1	0.7
	<i>Dythemis rufinervis</i> (Burmeister, 1839)**		0.9	5.6
	<i>Erythemis plebeja</i> (Burmeister, 1839)	2.9		
	<i>E. simplicicollis</i> (Say, 1839)	0.8		
	<i>Erythrodiplax berenice naeva</i> (Hagen, 1861)	0.2	0.2	0.2
	<i>E. fervida</i> (Erichson, 1848)	9.6	0.2	
	<i>E. justiniana</i> (Selys, 1857)**	3.5	0.2	0.2
	<i>E. umbrata</i> (Linnaeus, 1758)	3.3	2.3	0.5
	<i>Macrothemis celeno</i> (Selys, 1857)**	5.5	4.6	37
	<i>Miathyria marcella</i> (Selys, 1857)	6.9		
	<i>M. simplex</i> (Rambur, 1842)		2.3	0.2
	<i>Micrathyria aequalis</i> (Hagen, 1861)		0.5	
	<i>Orthemis ferruginea</i> (Fabricius, 1775)		9.5	1.7
	<i>Pantala flavescens</i> (Fabricius, 1798)	0.2		9.9
	<i>P. hymenaea</i> (Say, 1839)	0.2	1.4	17
	<i>Perithemis domitia</i> (Drury, 1773)	3.7		
<i>Scapanea frontalis</i> (Burmeister, 1839)**	3.2	0.9	6.3	
<i>Tauriphila australis</i> (Hagen, 1867)	0.2			
<i>Tramea abdominalis</i> (Rambur, 1842)		2.8	0.5	
<i>T. calverti</i> Muttikowski, 1910	0.4			

* Endemic to Cuba; – ** Endemic to The Antilles

logical and ethological features. Eight variables were recorded:

- (1) Labium shape as seen from the ventro-anterior surface of the head is either flat, slightly concave, or concave (Fig. 3).
- (2) Eyes position: frontal (1), dorsal (2), lateral (3), latero-dorsal (4).
- (3) Abdominal spines: absent (1), lateral (2), lateral and medio-dorsal (3) (Fig. 4 B).
- (4) Length of the third pair of legs (sum of the femur and tibia): 3.01-6mm (1), 6.01-9mm (2), 9.01-12mm (3), 12.01-15mm (4) (Fig. 4).
- (5) Total length/sum of the femur and tibia (Fig. 4): 1-3.5 (1), 3.51-6 (2).
- (6) Abdomen/head width: <1 (1), >1 (2) (Fig. 4).
- (7) Ovipositing behaviour: exophytic (1), endophytic (2), periphytic (3).
- (8) Microhabitat of the larvae: benthos (1), vegetation (2), rocks (3), benthos diggers (4).

A matrix with the state of every character for all species was built, to perform a cluster analysis with Euclidian distance and averaged binding (LEGENDRE & LEGENDRE, 1998). The average Euclidian distance was used to establish the groups, which were given names related to the morphological and behavioural characters of the species within each group. The dendrogram was obtained with STATISTICA® 8.0, StatSoft.

RESULTS

In the permanent lentic habitat (Las Cuabas), 504 exuviae (81% Anisoptera) were collected from 31 species (8 Zygoptera and 23 Anisoptera) in five families and 22 genera. In the temporary lentic habitat (Guasima), 434 exuviae (82% Anisoptera) were collected from 26 species (eight Zygoptera and 18 Anisoptera) in five families and 20 genera. In the lotic habitat 443 individuals (68% Anisoptera) were collected from 22 species (seven Zygoptera and 15 Anisoptera) in six families and 18 genera (Tab. I).

The cluster analysis allowed the delimitation of five morphofunctional groups for 41 species from six families (Fig. 5). The first clade, "Lamellates" is formed by the 12 species of Zygoptera, with three caudal lamellar branchiae as a distinctive character. The species lack abdominal spines, have lateral eyes rather than frontal, the head wider than the abdomen and the labium slightly concave. In

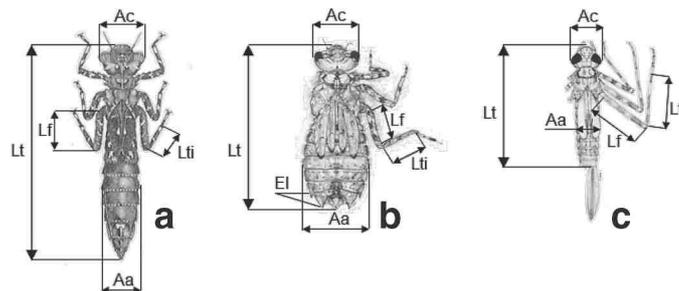


Fig. 4. Diagram of odonate exuviae, indicating the morphometrical variables measured: (a) Aeshniidae; – (b) Libellulidae; – (c) Coenagrionidae. – Lt: total length, – Lf: femur length, – Lti: tibia length, – Aa: abdomen width, – Ac: head width, – El: lateral spines. [Taken from CORBET, 1999 and NOVELO-GUTIÉRREZ, 1994].

Table II
Typical habitat, larval habit and oviposition of the odonate species collected in the three habitats, permanent and temporary lentic, and lotic

Families	Infrageneric taxa	Typical habitat	Larval habit	Oviposition	References
Lestidae	<i>Lestes forficula</i> <i>L. spumarius</i> <i>L. tenuatus</i>	Temporary lentic with emergent aquatic vegetation. Filtered insulation.	Climbers on emergent vegetation	Endophytic	Lutz (1968); Ingram (1976); Paulson (1982); Jödicke, 1997
Protoneuridae	<i>Neoneura maria</i> <i>Protoneura capillaris</i>	Permanent lotic with rocky-sandy bottom. Filtered insulation by gallery forests.	Climbers and/or graspers of rocks and vegetation	Endophytic (floating detritus), in tandem	Gloyd & Wright (1959) Pennak & Ward (1986)
Coenagrionidae	<i>Enallagma civile</i> <i>E. coecum</i> <i>Ischnura capreolus</i> <i>I. hastata</i> <i>I. ramburii</i>	Permanent lentic and lotic, with aquatic vegetation. Total insulation. Permanent lentic with aquatic vegetation. Total insulation. Permanent lentic and semi-lentic with aquatic vegetation. Total insulation.	Vegetation climbers Vegetation climbers Vegetation climbers	Endophytic, in tandem Endophytic, in tandem Endophytic, in tandem	Ingram & Jenner (1976) Westfall & May (1996) Kumar (1979) Westfall & May (1996) Johnson (1964)
	<i>Leptobasis vacillans</i> <i>Telebasis dominicanum</i>	Permanent lentic with aquatic vegetation. Partial insulation. Permanent lentic with aquatic vegetation. Total insulation.	Vegetation climbers Vegetation climbers	Endophytic, in tandem Endophytic, in tandem	Westfall & May (1996) Westfall & May (1996); Donnelly (1970); Runck & Blinn (1993)
Aeshnidae	<i>Anax amazili</i> <i>A. junius</i> <i>Coryphaeschna adnexa</i> <i>Gynacantha nervosa</i> <i>Triacanthagyna septima</i>	Permanent lentic with aquatic vegetation. Total insulation. Temporary lentic with aquatic vegetation. Filtered insulation.	Vegetation climbers Reptants in detritus	Endophytic, in tandem Endophytic, in tandem (fallen leaves, detritus)	Corbet (1999) Kime (1974) Wissinger (1988) Corbet (1999) Fincke (1992)
	<i>Rhionaeschna psilus</i>	Lentic with aquatic vegetation (lakes, marshes, swamps). Total insulation.	Vegetation climbers	Endophytic, in tandem	Calil & Carvalho (1999) Corbet (1999)
Gomphidae	<i>Aphylla caraiba</i> <i>Progomphus integer</i>	Permanent semi-lentic. Filtered insulation. Occasional lotic. Filtered insulation.	Diggers on thin sand Diggers on gravel	Exophytic Exophytic	Corbet (1999), Carvalho (1991) Corbet (1999); Novelo-Gutiérrez (2007)

Table II, continued

Families	Infrageneric taxa	Typical habitat	Larval habit	Oviposition	References
Libellulidae	<i>Cannaphila insularis funerea</i>	Lentic and permanent semi-lentic, with aquatic vegetation. Total insulation.	Reptant, mud digger	Exophytic	Limongi (1989)
	<i>Crocothemis servilia</i>	Lentic and permanent semi-lentic, with aquatic vegetation. Total insulation.	Reptant, thigmotactic	Exophytic	Corbet (1999); Sage (1960); Kumar (1976)
	<i>Dythemis rufinervis</i>	Permanent lotic. Filtered insulation.	Reptant, thigmotactic	Exophytic	Corbet (1999); Donnelly (1970)
	<i>Erythemis plebeja</i>	Permanent lentic with aquatic vegetation. Total insulation.	Climber on vegetation	Exophytic	Morin (1984b)
	<i>E. simplicicollis</i>				
	<i>Erythrodiplex berenice naeva</i>	Permanent brackish lentic. Total insulation.	Climber on vegetation.	Exophytic	Corbet (1999)
	<i>E. fervida</i>	Permanent lentic with aquatic vegetation. Total insulation.	Climber on vegetation.	Exophytic	Corbet (1999); Donnelly (1970)
	<i>E. justiniana</i>				
	<i>E. umbrata</i>				
	<i>Macrothemis celeno</i>	Lotic with rocky bottom and permanent lentic. Total insulation.	Reptant, thigmotactic	Exophytic	Ramírez & Novelo-Gutiérrez (1999)
	<i>Miathyria marcella</i>	Permanent lentic with aquatic vegetation			Bick (1953);
	<i>M. simplex</i>	(on <i>Elodea</i> , and roots of <i>Eichhornia crassipes</i>). Total insulation.	Climber on vegetation.	Exophytic	Limongi (1989)
	<i>Micrathyria aequalis</i>	Lentic with aquatic vegetation.	Reptant, thigmotactic	Epiphytic	Needham (1943)
	<i>Orthemis ferruginea</i>	Temporary lentic. Filtered insulation.	Reptant, mud digger	Exophytic	Smith & Pritchard (1956); Watson (1962); Corbet (1999)
	<i>Pantala flavescens</i>	Permanent lentic with aquatic vegetation			Paulson (1982); Kumar (1984);
	<i>P. hymenaea</i>	(<i>Cladophora</i>). Total insulation. Lotic.	Reptant, thigmotactic	Exophytic in tandem	Novelo et al. (1988); Corbet (1999)
	<i>Perithemis domitia</i>	Permanent lentic. Filtered insulation.	Reptant and climber	Exophytic	Corbet (1999); Santos (1981); Morin (1984a)
<i>Scapania frontalis</i>	Permanent lotic, with rocky-sandy bottom. Filtered insulation by gallery forests.	Reptant, thigmotactic	Exophytic	Corbet (1999)	
<i>Tauriphila australis</i>	Permanent lentic with aquatic vegetation. Total insulation.	Reptant, thigmotactic	Exophytic	Costa & Assis (1994); Trapero (2007)	
<i>Tramea abdominalis</i>	Permanent lentic with aquatic vegetation			Corbet (1999); Morin (1984b)	
<i>T. calverti</i>	(<i>Cladophora</i>). Total insulation.	Reptant, thigmotactic	Exophytic in tandem		

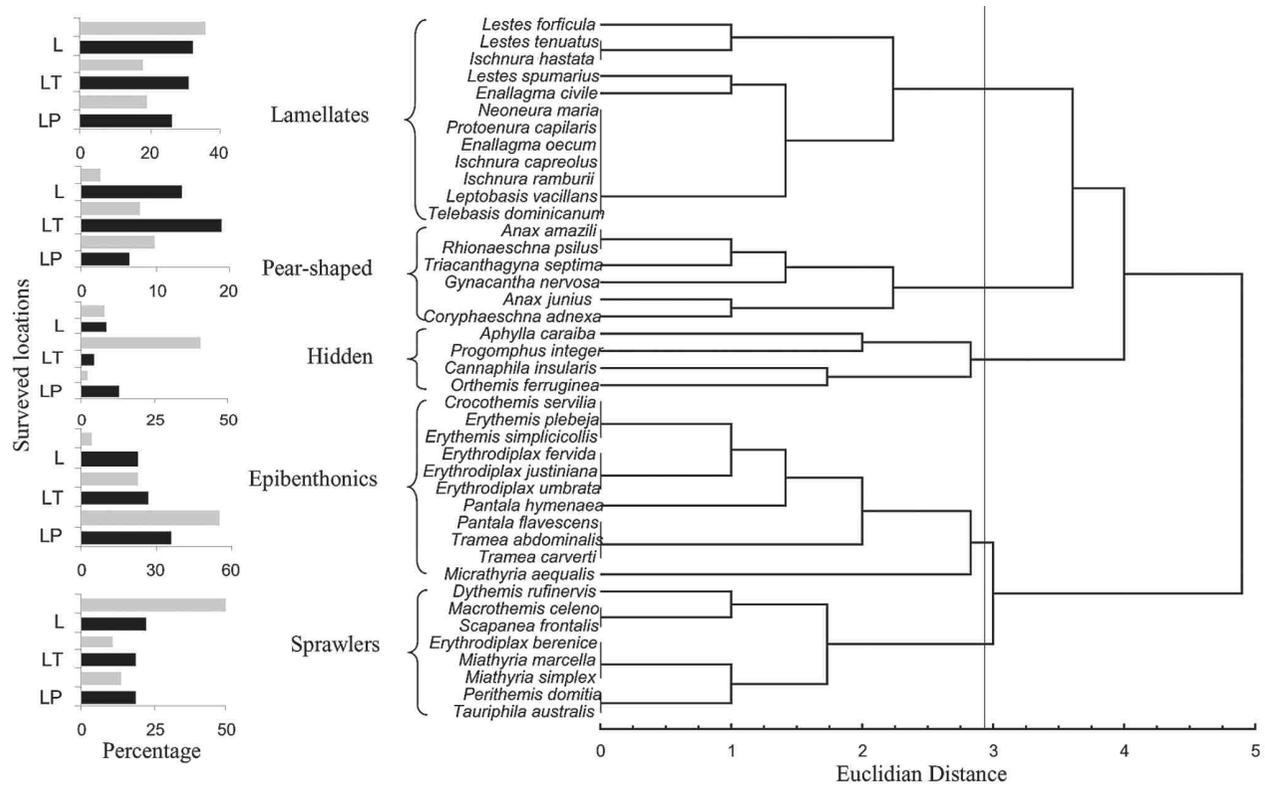


Fig. 5. Species richness and exuviae abundance of odonates in the morphofunctional groups in the three habitats: LP: permanent lentic, - LT: temporary lentic, - L: lotic. Left: abundance percentage per exuviae and species on each group. Black bars: percentage of species, gray bars: percentage of exuviae. The vertical line represents the average Euclidian distance (2.97).

this group the legs were never longer than 8mm, except for *Lestes forficula* in the temporary lentic habitat. The second group “Pear-shaped” is so called after the abdomen form; narrow in the anterior portion and wider behind. It is formed by the Aeshnidae species (Fig. 5), with lateral abdominal spines; eyes occupying the latero-dorsal surface of the head, the abdomen wider than the head, and a flat labium. The legs varied in length between 8 and 14 mm, except in *Gynacantha nervosa* where they were less than 8 mm long.

The third group named “Hidden” is the smallest group (centre) formed by four species, included the Gomphidae species, and the libellulids *Cannaphila insularis funerea* and *Orthemis ferruginea* (Fig. 5). They have dorso-frontal eyes; the abdomen is wider than the head, except in *C. insularis funerea*. The labium is flat in gomphids but concave in the libellulids. The leg length only exceeds 9 mm in *O. ferruginea*.

The remaining two groups are the Epibenthonics (11 species) (from *Crocothemis servilia* to *Micrathyria aequalis*) and the “Sprawlers” (eight species) (from *Dythemis rufinervis* to *Tauriphila australis*) (Fig. 5). Both groups have a tendency towards a hydrodynamic body and a concave labium covering the ventral and mid frontal surface of the head; the eyes occupy the latero-dorsal surface of the head. The larvae in the Epibenthonics have lateral abdominal spines only, while those in the Sprawlers also have mid-dorsal spines. Most of the species within the Epibenthonics have walking larvae and are benthos inhabitants. The Sprawlers, in contrast, were more frequently collected from rocks in freshwater habitats. The leg lengths varied less for this group and were between 6 and 9 mm, except in *Perithemis domitia* and *Tauriphila australis* where they were up to 11 mm. The Epibenthonics grouped those with the largest legs.

Most species were lamellates in both the temporary lentic and the lotic habitats. Indeed the Lamellates exceeded 25% of the species on every location (Fig. 5). The largest proportion of species varied within groups between habitats. The pear-shaped was always the least abundant with less than 10% of the exuviae in each habitat (Fig. 5). The Epibenthonics were dominant, in the permanent lentic (54.9%) and in the lotic the Sprawlers represented 49.8%. In the temporary lentic, the species *O. ferruginea* in the Hidden group had 40.7% of the exuviae. In every habitat the dominant group had more than 40% of the collected species, regardless of the species richness. The Libellulidae exhibited the largest diversity of morphofunctional groups.

DISCUSSION

According to CORBET (1980; 1983) odonates are a rather anatomically homogeneous group. Nevertheless, morphological differences are more conspicuous in the larval state, reflecting the myriad variety of environmental conditions and resources in their habitats (CARVALHO & NESSIMIAN, 1998). The only

work known to the authors that has considered the ecomorphological variation of odonate larval morphometry analyzed only 13 species of Libellulidae (GIACOMINI & DE MARCO, 2008). They noted that species which use vegetation have a larger labium and a narrower abdomen. A probable explanation for these differences would be the advantages in using resources and reducing vulnerability to predators.

Most of the Libellulidae species have reptant larvae in both lentic and lotic habitats, although some climb over plants (Tab. II). It is noticeable that these species occurred in three of the groups. The main difference between them in two of the groups was the presence/absence of abdominal spines, which might be associated with variation in vulnerability to predators, which was suggested by ARNQVIST & JOHANSSON (1998) and; MIKOLAJEWSKI & JOHANSSON (2004) for species in northern Europe. Another relevant variable was leg length, which distinguished those species best fitted to grasp and climb on substrates. However, in reptant species this was related to effectiveness in tactile detection of prey, as evaluated by PRITCHARD (1965) in species in this family. Two other libellulids, *Cannaphila insularis* and *Orthemis ferruginea*, remain semi-buried. These are closer to the Hidden group, whose main feature is dorsal eyes. Also, the four species in this group have long and cylindrical bodies with short legs, suitable for removing substrate as they burry themselves. In the gomphids, the body surface has neither hairs nor setae. On the other hand, pubescence is notable in the libellulids and allows retention of particles as camouflage. Furthermore, the eyes are elevated for the best detection of prey. This character was analyzed by WATSON (1962) and MISOF (2002) in species with similar behaviour and morphology.

In general, zygopterans inhabit lentic freshwater environments with aquatic vegetation, except for protoneturids which live in mountain streams. Nevertheless, some species from Protoneuridae have been recorded from lagoons and ponds, as noted by VON ELLENRIEDER & GARRISON (2009). Their larvae are climbers in roots, stems and rocks (Tab. II). Lestids have been recorded as essentially climbers and eventual swimmers (COSTA & CARNEIRO, 1994). However, STOKS & McPEEK (2003) showed segregation between species of *Lestes* in different kinds of freshwater habitats. Similarly, aeshnid larvae start as climbers in lentic bodies with vegetation cover, except for *Gynacantha nervosa* and *Triacanthagyna septima* which are reptant among detritus (Tab. II).

The analysis of the proportion of exuviae within groups proves the adaptive role of these larval characters. The epibenthonics were the most successful in the permanent lentic habitat. The presence of lateral spines and more variability in leg length are an evolutionary response to the presence of small fish. Despite *Gambusia punctata*'s diet including insects and their larvae (FONG et al., 1996) its foraging behaviour is mainly close to the water surface (RODRÍGUEZ, 2007). This behaviour partly explains the successful coexistence between odonates and vertebrates in this habitat. Additionally, the Sprawlers in the lotic habitat were

more likely to complete their life cycle in presence of larger fish like *Nandopsis tetracanthus*. Such coexistence increases the adaptive value of the mediadorsal spines. Its shape and length might be modulated by natural selection, as a morphological strategy to avoid predation. This finding is in accord with those of JOHANSSON & SUHLING (2004) and McPEEK (2008) in Europe and North America.

On the other hand, in the temporary lentic habitat, *Orthemis ferruginea* from the Hidden group represented 40.7% of the individuals. The absence of fish in this environment assures the biological efficiency of this species lacking prominent spines, laying semi-buried in the substrate. This illustrates the limited effect of these vertebrates in the specific abundance distribution, also noted by WISEMAN et al. (1993) and DIJKSTRA & LEMPERS (2003). *Orthemis ferruginea* is probably the main predator in this habitat.

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REFERENCES

- ARNQVIST, G & F. JOHANSSON, 1998. Ontogenetic reaction norms of predator-induced defensive morphology in dragonfly larvae. *Ecology* 79(6): 1847-1858.
- ASAHINA, S., 1950. On the life-history of *Epiophlebia superstes* (Odonata: Anisozygoptera). *Proc. 8th Int. Congr. Ent.*, Stockholm, pp. 337-341.
- BICK, G., 1953. The nymph of *Miathyria marcella* (Selys) (Odonata: Libellulidae). *Proc. ent. Soc. Wash.* 55(1): 30-36.
- CALIL, E. & A. CARVALHO, 1999. Descrições da larva de último estágio e do adulto de *Triacanthagyna septima* (Selys, 1857) (Odonata: Aeshnidae), com notas sobre a biologia da espécie. *Revta bras. Ent.* 43(1): 73-83.
- CALVERT, P., 1911. Studies on Costa Rican Odonata I. The larva of *Cora*. *Ent. News* 22: 49-64.
- CAPOTE, R. & R. BERAZAÍN, 1984. Clasificación de las formaciones vegetales de Cuba. *Revta Jard. Bot. nac.* 5(2): 1-49.
- CARVALHO, A., 1991. Notas sobre a odonofauna de restinga, em Maricá, Rio de Janeiro (Insecta, Odonata). *Revta bras Biol.* 51(1): 197-200.
- CARVALHO, A. & J. NESSIMIAN, 1998. Odonata do Estado do Rio de Janeiro, Brasil: hábitos e hábitos das larvas. In: J. Nessimian & A. Carvalho, [Eds], *Ecologia de insetos acuáticos*, Vol. 5: 3-28.
- CORBET, P.S., 1957. The life-history of the Emperor Dragonfly *Anax imperator* Leach (Odonata: Aeshnidae). *J. Anim. Ecol.* 26: 1-69.
- CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
- CORBET, P.S., 1980. Biology of Odonata. *Annu. Rev. Ent.* 25: 189-217.
- CORBET, P.S., 1983. Odonata in phytotelmata. In: J. Franck & L. Lounibos, [Eds.], *Phytotelmata: terrestrial plants as hosts of aquatic insect communities*, pp. 29-54, Plexus, Marlton/NJ.

- CORBET, P.S., 1999. *Dragonflies: behavior and ecology of Odonata*. Cornell Univ. Press, New York.
- COSTA, J. & C. ASSIS, 1994. Description of the larva of *Tauriphila australis* Hagen, 1867, from São Paulo, Brazil (Anisoptera: Libellulidae). *Odonatologica* 23(1): 51-54.
- COSTA, J. & S. CARNEIRO, 1994. Duas novas larvas de *Lestes* Leach e dados morfológicos sobre *Lestes pictus* Hagen (Odonata, Zygoptera, Lestidae). *Revta bras. Zool.* 11(2): 303-309.
- DIJKSTRA, K. & J. LEMPERS, 2003. Odonate assemblages of running waters in the Upper Guinean forest. *Arch. Hydrobiol.* 157: 397-412.
- ESQUIVEL, C., 2006. *Libélulas de Mesoamérica y el Caribe*. Inst. Nac. Biodiv., Santo Domingo/ Costa Rica.
- FONG, A. G. GARCÉS & E. PORTUONDO. 1996. Invertebrados en la alimentación de *Gambusia punctata* (Cyprinodontiformes: Poeciliidae) en aguas marinas. *Cocuyo* (5): 13-14.
- GIACOMINI, H. & P. DE MARCO. 2008. Larval ecomorphology of 13 Libellulidae (Anisoptera, Odonata) of the Middle Rio Doce Valley, Minas Gerais, Brazil. *Braz. J. Biol.* 68(1): 211-219.
- HIROSE, K. & M. ROKUYAMA, 1963. Two types of the larva of *Mnais strigata* and their distribution in the streams. *Tombo* 9: 23-27.
- INGRAM, B., 1976. Life histories of three species of Lestidae in North Carolina, United States (Zygoptera). *Odonatologica* 5: 231-244.
- INGRAM, B. & C. JENNER, 1976. Life histories of *Enallagma hageni* (Walsh) and *E. aspersum* (Hagen) (Zygoptera: Coenagrionidae). *Odonatologica* 5: 331-345.
- JÖDICKE, R., 1997. *Die Binsenjungfern und Winterlibellen Europas (Lestidae)*. Westarp, Magdeburg.
- JOHANSSON, F. & T. BRODIN, 2003. Effects of fish predators and abiotic factors on dragonfly community structure. *J. Freshw. Ecol.* 18(3): 415-423.
- JOHANSSON, F., P.H. CROWLEY & T. BRODIN, 2005. Sexual size dimorphism and sex ratios in dragonflies. *Biol. J. Linn. Soc.* 86: 507-513.
- JOHANSSON, F. & F. SUHLING. 2004. Behaviours and growth of dragonfly larvae along a permanent to temporary water habitat gradient. *Ecol. Ent.* 29: 196-202.
- JOHNSON, D. & P. CROWLEY, 1980. Odonate "hide and seek": habitat specific rules? In: W. Kerfoot, [Ed.], *The evolution and ecology of zooplankton populations*, pp. 565-579. Univ. Press New England, Hanover.
- KIME, J., 1974. *Ecological relationships among three species of aeshnid larvae (Odonata: Aeshnidae)*. PhD thesis. Univ. Washington, Seattle.
- KUMAR, A., 1976. Biology of Indian dragonflies with special reference to seasonal regulation and larval development. *Bull. Ent.* 17: 37-47.
- KUMAR, A., 1979. On the occurrence of multivoltine generations in some Indian dragonflies. *Sci. Cult.* 45: 126-127.
- KUMAR, A., 1984. On the life history of *Pantala flavescens* (Fabricius) (Libellulidae: Odonata). *Ann. Ent.* 2: 43-50.
- LEGENDRE, P. & L. LEGENDRE, 1998. *Numerical ecology*. Elsevier Science, Amsterdam.
- LIMONGI, J., 1989. Estudio morfo-taxonómico de náyades de algunas especies de Odonata (Insecta) en Venezuela (2). *Mems Soc. Cienc. nat. La Salle* 49: 405-419.
- LUTZ, P., 1968. Life history studies of *Lestes eurinus* Say (Odonata). *Ecology* 49: 576-579.
- McPEEK, M., 2008. Ecological factors limiting the distributions and abundances of Odonata. In: A. Córdoba-Aguilar, [Ed.], *Dragonflies and damselflies, model organisms for ecological and evolutionary research*, pp. 51-62. Oxford Univ. Press.
- MIKOLAJEWSKI, J. & F. JOHANSSON, 2004. Morphological and behavioral defenses in dragonfly larvae: trait compensation and cospecialization. *Behav. Ecol.* 15(4): 614-620.
- MISOFF, B., 2002. Diversity of Anisoptera (Odonata): adducing speciation processes from patterns of morphological diversity. *Zoology* 105: 355-365.
- MORIN, P., 1984a. The impact of fish exclusion on the abundance and species composition of larval odonates: results of short term experiments in a North Carolina farm pond. *Ecology* 65: 53-60.

- MORIN, P., 1984b. Odonate guild composition: experiments with colonization history and fish predation. *Ecology* 65: 1866-1873.
- NEEDHAM, J., 1943. Life history notes on Micrathyria (Odonata). *Ann. ent. Soc. Am.* 36: 185-189.
- NEEDHAM, J. & M. WESTFALL, 1955. *A manual of the dragonflies of North America (Anisoptera) including the Greater Antilles and the provinces of the Mexico border*. Univ. Calif. Press, Berkeley.
- NEEDHAM, J., M. WESTFALL & M. MAY, 2000. *Dragonflies of North America*. Scient. Publishers, Gainesville/FL.
- NOVELO-GUTIÉRREZ, R., 1994. Las náyades de *Protoneura aurantiaca* Selys y *P. cupida* Calvert (Odonata: Zygoptera: Protoneuridae). *Fol. ent. mex.* 90: 25-31.
- NOVELO-GUTIÉRREZ, R., 2007. *Progomphus lambertoi* (Anisoptera: Gomphidae), a new species from Mexico. *Proc. ent. Soc. Wash.* 109(4): 791-797.
- NOVELO-GUTIÉRREZ, R., 2009. Description of the larva of *Acanthagrion quadratum* Selys, with a key to the known larvae of the genus (Zygoptera: Coenagrionidae). *Odonatologica* 38(4): 321-328.
- NOVELO-GUTIÉRREZ, R., O. CANUL-GONZÁLEZ & J. CAMAL-MEX, 1988. Los odonatos del estado de Quintana Roo, México (Insecta: Odonata). *Fol. ent. mex.* 74: 13-68.
- PAULSON, D., 1982. Odonata. In: S. Hurlbert & A. Villalobos-Figueroa, [Eds], *Aquatic biota of Mexico, Central America and West Indies*, pp. 249-278, San Diego St. Univ., San Diego/CA.
- PENNAK, R. & J. WARD, 1986. Interstitial faunal communities of the hyporheic and adjacent groundwater biotopes of a Colorado mountain stream. *Arch. Hydrobiol.* 74: 356-396.
- PRITCHARD, G. 1965. Prey capture by dragonfly larva. *Can. J. Zool.* 43: 271-289.
- RAEBEL, E., T. MERCKX, P. RIORDAN, D. MACDONALD & D. THOMPSON, 2010. The dragonfly delusion: why it is essential to sample exuviae to avoid biased surveys. *J. Insect Conserv.* 1-7.
- RAMÍREZ, A., 1997. Description and natural history of the Costa Rica Odonata larvae. 5. *Megaloprepus caerulatus* (Drury, 1782) (Zygoptera: Pseudostigmatidae). *Odonatologica* 26: 75-81.
- RAMÍREZ, A. & R. NOVELO-GUTIÉRREZ, 1999. The Neotropical dragonfly genus *Macrothemis*: new larval description and an evaluation of its generic status based on larval stages (Odonata: Libellulidae). *Jl N. Am. benthol. Soc.* 18(1): 67-73.
- RODRÍGUEZ, R. 2007. *Ecología de los peces del arroyo Govea, Bejucal, provincia de La Habana*. Tesis Licenc. Univ. La Habana, Ciudad de La Habana, Habana.
- RUNCK, C. & D. BLINN, 1993. Secondary production by *Telebasis salva* (Odonata) in thermally constant aquatic ecosystem. *Jl N. Am. benthol. Soc.* 12: 136-147.
- SAGE, B., 1960. Notes on the Odonata of Iraq. *Iraq nat. Hist. Mus. Publ.* 18: 1-11.
- SANTOS, N., 1981. Odonata. In: S. Hurlbert, G. Rodríguez & N. Santos, [Eds], *Aquatic biota of tropical South America*, 1: *Arthropoda*, pp. 64-85, San Diego St. Univ., San Diego/CA.
- SMITH, R. & A. PRITCHARD, 1956. Odonata. In: R. Usinger, [Ed.], *Aquatic insects of California*, pp. 106-153, Univ. Calif. Press, Berkeley.
- SOLUK, D., 1990. Postmolt susceptibility of Ephemera larvae to predatory stoneflies – constraints on defensive armor. *Oikos* 58(3): 336-342.
- STOKS, R. & M. McPEEK, 2003. Antipredator behavior and physiology determine *Lestes* species turnover along the pond-permanence gradient. *Ecology* 84: 3327-3338.
- TILLYARD, R.J., 1917. *The biology of dragonflies (Odonata: or Paraneuroptera)*. Cambridge Univ. Press.
- TRAPERO, A., 2007. *Macroinvertebrados asociados a las raíces de Eichhornia crassipes (Pontederiaceae), en la represa Chalons, Santiago de Cuba*. Tesis Maest., Univ. La Habana, Habana.
- TRAPERO, A. & C. NARANJO, 2009. Clave para la identificación de especies de Odonata en estado larval de Cuba. *Boln Soc. ent. aragon.* 44: 459-467.
- TROTTIER, R., 1973. Influence of temperature and humidity on the emergence behaviour of *Anax junius*. *Can. Ent.* 105: 975-984.

- VON ELLENRIEDER, N. & R. GARRISON, 2009. Odonata. In: E. Domínguez & H. Fernández, [Eds.], *Macroinvertebrados bentónicos sudamericanos: sistemática y biología*, pp. 95-143, Fundación Miguel Lillo, Tucumán.
- WATSON, J., 1962. *The dragonflies (Odonata) of south-western Australia: a guide to the identification, ecology, distribution and affinities of larvae and adults*. W. Aust. Naturalists' Club, Perth.
- WATSON, J., 1982. A truly terrestrial dragonfly larva from Australia (Odonata: Corduliidae). *J. Aust. Ent.* 21: 309-311.
- WESENBERG-LUND, C., 1913. Odonaten-Studien. *Int. Revue Hydrobiol.* 6: 155-228.
- WESTFALL, M. & M. MAY, 1996. *Damselflies of North America*. Scient. Publishers, Gainesville/FL.
- WILLIAMS, F., 1936. Biological studies in Hawaiian water-loving insects, 2: Odonata or dragonflies. *Proc. Hawaii. ent. Soc.* 9: 273-349.
- WINSTANLEY, W., 1984. The larva of the New Caledonian endemic dragonfly *Synthemis ariadne* Lieftinck (Anisoptera: Synthemistidae). *Odonatologica* 13: 159-164.
- WISEMAN, S., S. COOPER & T. DUDLEY, 1993. The effects of trout on epibenthic odonate naiads in stream pools. *Freshw. Biol.* 30: 133-145.
- WISSINGER, S., 1988. Life history and size structure of larval dragonfly populations. *Jl N. Am. benthol. Soc.* 7: 13-28.
- ZAHNER, R., 1959. Über die Bindung der mitteleuropäischen Calopteryx-Arten (Odonata: Zygoptera) an den Lebensraum des strömenden Wassers, 1: der Anteil der Larven an der Biotopbindung. *Int. Revue Hydrobiol.* 44: 51-130.

**OVIPOSITION BEHAVIOUR IN THE DRAGONFLY
SYMPETRUM INFUSCATUM (SELYS) MISTAKING DRIED-UP
RICE PADDY FIELDS AS SUITABLE OVIPOSITION SITES
(ANISOPTERA: LIBELLULIDAE)**

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Tandem oviposition behaviour of *S. infuscatum* was studied in rice paddy fields that were dried due to agricultural procedures in the cool temperate zone of Japan. Oviposition site selection is probably mainly visual because every tandem pair is attracted to structurally similar rice paddy fields without any water. Observations of flying behaviour of tandems was carried out on sunny days without winds. All pairs flew about to search for a suitable oviposition site in the rice paddy fields. They hovered to start oviposition while in tandem. ♀♀ of tandems flicked their abdomen while on the wing to aid egg release; each height of these oviposition flights was measured. They separated after completion of the oviposition bout. Vertical changes in the air temperature, relative humidities and light intensities above and below the top of the rice plants were measured. Oviposition site selection was related to the vertical decline of vapour pressure above the rice plants, suggesting that the horizontal surface of rice paddy fields horizontally reflects highly polarized light. Eggs that had fallen on dried-up rice paddy soil diapaused throughout the winter and started to develop the following spring when the field was filled with enough water for rice planting. Therefore, there is a mechanism for suitable habitat selection for larval development under seasonal changes in man-made water supplies for the cultivation of rice plants.

INTRODUCTION

Patterns of female oviposition behaviour that place offspring in favourable conditions are critical for odonate species, due to the ecological requirements of their aquatic larvae. Because desiccation is one of the common sources of mor-

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tality for eggs and larvae, females have to produce batches of mature eggs, mate, carefully select appropriate oviposition sites and deposit their eggs (FINCKE, 1992; SCHENK et al., 2004).

Every female dragonfly has limited ability to influence the survival of offspring after egg deposition since no parental care is provided, suggesting strong selection pressure to choose oviposition sites in which larval survival is high. BUSKIRK & SHERMAN (1984) stated that such sites are characterized by physical conditions that are favourable for larval development, i.e. that provide sufficient food for larvae, that minimize predation, and that minimize intra- and interspecific larval competition. MICHIELS & DHONDT (1990) pointed out that the mortality from egg to adult in Odonata was more than 90%. However, females are unable to assess predator density or relative food supply for larvae. Therefore, they must use general habitat cues to evaluate oviposition site quality.

Although CORBET (1999) reviewed the variation of oviposition behaviour in Odonata, using functional and behavioural criteria, the females of a few species release eggs on the wing above water. SILSBY (2001) noticed two *Sympetrum* species dropping their eggs over dry land, generally into long grasses growing at various distances from the water. Among *Sympetrum* species in Japan, however, aerial dropping of eggs by females is commonly observed in *S. infuscatum*, *S. darwinianum*, *S. r. risi* and *S. maculatum* (MIZUTA, 1978). Such dragonflies move freely about rice paddy fields that are dried up (WATANABE & TAGUCHI, 1988). During oviposition, females discharge their eggs while flying in tandem over the rice paddy fields.

Eggs of most odonate species are released by dipping or flicking into water or mud, or are inserted into aquatic plant tissues. Females do not normally lay eggs on dry surfaces, though remarkable mistakes occur at certain artificial surfaces such as car bodies (HORVATH et al., 2007). WILDERMUTH (1998) stated that dragonflies detect their oviposition sites using visual cues, primarily by the use of polarized light that is reflected at the surface of still water, i.e. polarotaxis is an essential part of the process. However, KOSUGI (2000) observed *S. frequens* ovipositing on an iron plate glittering on a sunny day. Also a male *Libellula depressa* has been observed to mistake a dark-green passenger coach for a water body (WILDERMUTH & HORVATH, 2005). MUTO (1981) pointed out that the cue releasing oviposition behaviour on the shiny horizontal roof of a vehicle by *Pantala flavescens* was the reflection of horizontally polarized light resembling the corresponding pattern at a water plane. Therefore, some dragonfly species are polarotactic and detect water by means of horizontally polarized light reflected from the surface of water (WATSON, 1992). Thus, they could be deceived by any surface with similar polarization features. However, *Sympetrum infuscatum* uses rice paddy fields for oviposition. These dry up due to the cultivation procedures of rice plants and there seems to be no surface on rice plants that have specific polarization features. CORBET (1999) stated that oviposition behaviour on a

dry surface is linked with hatching that is delayed until the surface is naturally flooded.

The objective of this paper is to describe the selection pressures in *S. infuscatum* acting on oviposition behaviour that are directly related to the survival of their offspring. In particular, we are concerned with where and how the female releases her eggs on dry land. As noted above, the dried up rice paddy fields seem not to have surfaces that reflect horizontally polarized light. Thus the effects of site orientation and the vertical changes in abiotic environment in the rice paddy fields were examined, to determine cues by which *S. infuscatum* adults identify the suitability of substrates as egg-laying places. In addition, our approach considers the conservation ecology of the dragonfly in order to predict the optimum oviposition behavior in relation to seasonal changes in man-made water conditions of rice paddy fields.

SPECIES

There is little quantitative information on mating and oviposition behaviour and oviposition site selection in *S. infuscatum*. Copulation is considered to occur on the crowns of cedar along forest margins. When a male captures the female, a period of tandem flight formation might be seen, followed by perching in a copulatory wheel. The pair remain in tandem after the termination of copulation and may fly over a large area toward the rice paddy fields, though the fields are dry.

Every female arrives in the rice paddy fields in tandem and starts to oviposit over rice plants, with some wandering above the rice paddy fields. Prior to the moment of oviposition, tandem pairs fly about, presumably in search of suitable oviposition sites in rice paddy fields. During oviposition, tandem pairs hover constantly at the same height above the rice plants while the female regularly flicks her abdomen to discharge eggs without touching the rice plants. This behaviour may be interpreted as assessing the physical properties of the vertical change in air conditions. Each pair does not maintain a territory around the oviposition site. The eggs are desiccation resistant (WATANABE, 1996) and do not hatch until covered by water the following spring.

MATERIAL AND METHODS

The study site was in rice paddy fields (1.5 km²), surrounded by mountains covered by artificially planted cedar forests in the Kamishiro region, Shirouma, Nagano, Japan (WATANABE et al., 2004). Field work was carried out for eight hot, windless and clear sky days in late August 2010 on the selected rice paddy field (3696 m²), where the reproductive activities of *S. infuscatum* were concentrated (WATANABE et al., 2005). The rice paddy fields are generally completely dry after mid-August every year. The heights of the rice plants were constantly 90 cm in height with many ears of rice. No water was found, except for the margins of the rice paddy fields where there was moisture-rich mud that provided an oviposition site for *S. frequens*.

For the survey, a straight line of 84 m along the rice paddy field was chosen. To obtain information

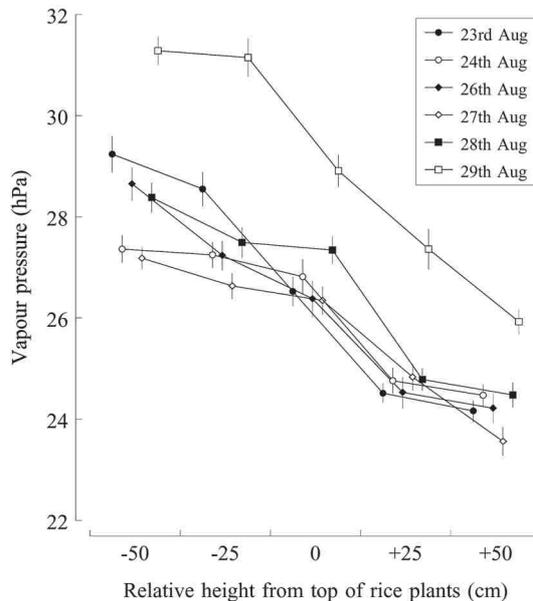


Fig. 1. Vertical changes in vapour pressure of the rice paddy fields during the oviposition flight period (10:00-13:00) of *Sympetrum infuscatum* in late August 2010. The height of the rice plants was about 90 cm. Each day was sunny with little wind.

not involved in oviposition, their flight speed was high and they were soon out of sight.

Inside the rice paddy fields, automatic recorders for temperature and humidity were vertically mounted on a pole 2 m high: +50 cm, +25 cm, 0 cm, -25 cm, -50 cm from the top of the rice plants (90 cm). Ambient air temperature during each 15 min session was also measured at 1.35m using an Assmann psychrometer. The probes measuring light intensity were set up in an open area on the top of the rice plants, parallel with the soil and perpendicular to the sun's rays. The wind velocity was also measured at 90 cm above ground.

RESULTS

During the survey period, we noted many individuals of three dragonfly species in the paddy fields, even though a body of water was lacking. For *S. infuscatum* and *S. frequens*, mature and reproductively active individuals of both sexes were present, though some juveniles of *Pantala flavescens* were also present. The three species can easily be distinguished, using morphology and behaviour.

During the observation period between 10:00 - 13:00, the ambient air temperature was around 30°C (Tab. I), the relative humidity was about 75%, and the vapour pressure was around 25 hPa. There was little cloud cover and the light

about the frequency of oviposition behaviour, we recorded how many tandems were ovipositing along that line. Although the data are based on observations of unmarked pairs, each tandem was easily identified because of their hovering behaviour. All observations were made by eye or with the aid of binoculars.

Because visiting rice paddy fields for oviposition of *S. infuscatum* is restricted to the morning until noon, occurrence of tandem pairs, lone males, and other dragonflies in the study rice paddy fields were individually noted as to their flight height over the rice paddy fields from 10:00 to 13:00, during which high activity of oviposition is found. Each recording was made at 15 min intervals, walking along the straight line in the rice paddy field. Flying behaviour of pairs was arbitrarily classified into two groups. 'Ovipositing' was when the pair hovered with dipping movements. 'Moving' means that a pair flew slowly without dipping. The number of pairs that flew more than 2 m over the rice plants was not counted because they were

Table I
Air temperature, vapour pressure and light intensity above the rice paddy fields measured by using Assmann psychrometer (\pm SE)

Date	Air temperature ($^{\circ}$ C)	Vapour pressure (hPa)	Light intensity (\times 100 lx)
23rd Aug	31.0 \pm 0.2 (13)	26.3 \pm 0.2 (13)	1091.8 \pm 114.0 (14)
24th Aug	31.1 \pm 0.3 (13)	25.4 \pm 0.5 (13)	1071.2 \pm 103.9 (14)
26th Aug	28.9 \pm 0.2 (13)	24.0 \pm 0.3 (13)	1145.8 \pm 88.9 (14)
28th Aug	30.8 \pm 0.2 (13)	25.9 \pm 0.2 (13)	-
29th Aug	29.6 \pm 0.3 (13)	25.6 \pm 0.3 (13)	-

(): Number of samples that measured each 15min during 10:00-13:00

intensity was more than 100,000 lx. Those data were obtained at a height of 135 cm above the open grassland next to the rice paddy fields. The height of the grass was less than 10 cm. Above the rice plants, the wind velocity was always lower than 2 m/s.

The height of every rice plant in the study rice paddy fields was 90 cm and the plants had ripened. There were vertical changes of the air temperature due to the added radiation temperature against the sensor of the auto thermorecorders; that is, higher than 30 $^{\circ}$ C above the rice plants and about 30 $^{\circ}$ C inside the rice plant community. The humidity also changed vertically. Figure 1 shows the vertical changes in the vapour pressure in each observation day. Although the vapour pressure at -50 cm and -25 cm in height from the top of rice plants were not significantly different a drastic decline was found at the height of 0 cm (Tab. II).

S. infuscatum pairs did not localize their flights at oviposition sites. Instead, they flew over large portions of the rice paddy field in a short period of time. Several pairs were frequently seen within several metres of each other. However, chases between pairs were rare. Pairs that flew to within 1 m of another pair usually altered their flight path to avoid the pair. Few ovipositions were disturbed by conspecific single males or by *S. frequens* males, or by birds and wasps. During

Table II
Results of multiple comparison analysis among each height for vapour pressure shown in Fig. 1 (Dunnnett T3 test)

Height	-50cm: -25cm	-25cm: 0cm	0cm: 25cm	25cm: 50cm
23rd Aug	$p = 0.89$	$p < 0.01$	$p < 0.01$	$p = 0.92$
24th Aug	$p = 1.00$	$p = 0.99$	$p < 0.01$	$p = 1.00$
26th Aug	$p = 0.02$	$p = 0.50$	$p < 0.01$	$p = 1.00$
27th Aug	$p = 0.83$	$p = 0.99$	$p = 0.04$	$p = 0.20$
28th Aug	$p = 0.35$	$p = 1.00$	$p < 0.01$	$p = 0.99$
29th Aug	$p = 1.00$	$p < 0.01$	$p = 0.04$	$p = 0.04$

undisturbed ovipositions, pairs hovered above the rice plants for the entire oviposition sequence. A small number of pairs abruptly moved a short distance to a new oviposition site in the same rice paddy field. Since the oviposition duration of each pair was less than 10 min, pairs ovipositing in each 15 min count were not the same. Females released from tandem pairs were chased by other lone males as they left the rice paddy fields. No females were captured by the lone males, eventually with no further oviposition in tandem. No factor was identified that influenced the timing of separation within any one oviposition sequence.

The number of dragonflies counted changed within and between survey days. During the survey period, 10:00-13:00, no specific time of arrival at the rice paddy fields was observed for tandem pairs of *S. infuscatum*, though lone males were apt to stay for foraging but not for harassing tandems. Little interference between tandems were found, probably due to low densities (Tab. III). The number of tandems of *S. frequens* was lower than that of *S. infuscatum*, because they were restricted to the margins of the rice paddy fields, in which a little water in the mud provided for oviposition sites. Since every tandem dived down toward the ground level of the rice paddy fields, the micro habitat was quite different for ovipositing tandems of *S. frequens* and *S. infuscatum*. A mass flight of *P. flavescens* was sometimes observed during the survey period. Since their flight height was more than 5m above the rice paddy fields, there was no interaction with either *S. infuscatum* or *S. frequens*.

Ovipositing females held by a male usually remained very low above the rice plants. As shown in Table IV, pairs hovered ca. 3 cm above the rice plants, while the height of moving pairs was significantly higher (around 20 cm above the rice plants).

Table III

The number of tandems ovipositing and moving, and the number of lone males of *Sympetrum infuscatum*, and the number of tandems and males of *S. frequens* for each census of 84m in the rice paddy field (\pm SE). There were no lone females of either species.

Date	No. census	No. tandems ovipositing	<i>S. infuscatum</i>		<i>S. frequens</i>	
			No. tandems moving	No. lone males	No. tandems	No. lone males
23rd Aug	13	1.0 \pm 0.4	1.6 \pm 0.5	4.5 \pm 0.9	0.3 \pm 0.1	0.3 \pm 0.2
24th Aug	13	0.5 \pm 0.3	0.0 \pm 0.0	2.1 \pm 0.7	0.1 \pm 0.1	0.0 \pm 0.0
26th Aug	13	2.1 \pm 1.1	0.1 \pm 0.1	4.2 \pm 1.2	0.3 \pm 0.3	2.3 \pm 0.6
27th Aug	13	4.2 \pm 1.0	2.2 \pm 0.8	2.0 \pm 0.6	0.2 \pm 0.2	0.3 \pm 0.2
28th Aug	13	4.8 \pm 1.0	1.0 \pm 0.3	7.4 \pm 0.9	0.1 \pm 0.1	0.0 \pm 0.0
29th Aug	13	3.0 \pm 0.9	2.6 \pm 0.8	4.3 \pm 1.1	0.8 \pm 0.5	0.5 \pm 0.3

Table IV
Flight height for ovipositing and moving of tandem above the top of rice plants

Date	Ovipositing (cm)	Moving (cm)	U-test	
23rd Aug	1.5±3.8 (13)	25.9±14.4 (21)	U = 5.0	p < 0.01
24th Aug	2.5±4.2 (6)	-	-	-
26th Aug	1.5±4.6 (27)	20.0 (1)	U = 0.5	p = 0.07
27th Aug	2.4±4.7 (54)	20.0±17.5 (29)	U = 186.5	p < 0.01
28th Aug	3.0±6.3 (62)	25.4±20.7 (13)	U = 95.5	p < 0.01
29th Aug	3.8±7.9 (39)	21.0±12.7 (34)	U = 140.0	p < 0.01

(): Number of tandems observed

DISCUSSION

Many aquatic insects recognize their natural habitat on the basis of the highly and horizontally polarized light reflected from the water surface (SCHWIND, 1991). In the ventral eye of the dragonfly, the retinula cells which exhibit maximum sensitivity in the UV range are highly sensitive to polarized light (LAUGHLIN, 1976). The orange receptor cells in the ventral retinula of *S. rubicundulum* were reported to be sensitive to polarized light (MEINERZHAGEN et al., 1983). Thus, for oviposition, odonate adults might find the water by polarotaxis rather than by thermotaxis, chemotaxis or negative phototaxis (WILDERMUTH, 1998). HORVATH (1995) pointed out that the polarization pattern of the aquatic habitat depends not only on the water surface but also on the light conditions in the sky. Therefore, visual habitat recognition by dragonflies is based on the pattern of polarized light and on structural properties determined by suspended particles (WILDERMUTH, 1998). In the present study, change in vapor pressure had an important factor for the water content in the air, probably affecting the polarization of light reflected from the moist air at the top of the rice plants. High moisture air layers must resemble water bodies because the layer has structures that show the homogeneous surface plane due to the equal height of the rice plants and due to the stable vapour pressure derived from the photosynthesis of the rice plants growing at equal rates. Positive polarotaxis could explain their attraction to horizontally polarizing air. However, the moisture rich air layer above the rice plants does not reflect highly polarized light during cloudy days nor during windy days or during low temperatures. Therefore, around noon on sunny days without wind are attractive periods for *S. infuscatum* for ovipositing activity.

WILDERMUTH & HORVATH (2005) reported that light reflected from a car surface can be mistaken for a water body. The smooth surfaces of perspex plates, plastic sheets and aluminum foil revealed that the plane horizontal polarization of the reflected light is important for oviposition (WILDERMUTH, 1998). However, the surface roughness of substrates influences the reflection-polarizational

characteristics (WILDERMUTH & HORVATH, 2005). Since rough surface reflects light diffusely, which reduces polarization, the variable height of natural grasslands decreases the degree of linear polarization of reflected light. Each component species in the grassland community may show respective efficiency of photosynthesis, resulting on different degrees of vapour pressure around each individual plant body. Therefore, natural grassland does not serve as oviposition sites for *S. infuscatum* due to none plane polarization.

Several aspects of female oviposition behaviour would affect survival of eggs and larvae, including temporal patterns, microhabitat choice and spatial dispersal of eggs. In addition, the behaviour of females would be affected by two primary causes of interrupted oviposition, that is, predation on the female and disturbance by conspecific males. Temporal aspects of oviposition primarily involve selective forces on the females. Bird predation on the dragonflies during the survey period 10:00-13:00 was sometimes observed above the rice paddy fields. Because each flight pass of birds was a considerable height above the rice plants, ovipositing tandems seemed not to be a target. Low male density also resulted in little disturbance of tandem ovipositions. Therefore, tandems must freely select their oviposition site in the rice paddy fields.

The two most common sources of mortality for eggs and larvae are predation and desiccation. Although the warmer water temperatures of shallow rice paddy fields would facilitate rapid growth of the larvae (BUSKIRK & SHERMAN, 1984), the cultivating schedule of rice paddy fields means that they dry up before the ripening of the rice in July, which is just after the completion of larval development. After emergence, *S. infuscatum* adults spend more than one month staying in forest gaps throughout their immature stage. Thus, oviposition at this stage in the rice paddy fields without water would increase the risk of desiccation. Thus eggs that have to survive prolonged periods of desiccation may require greater parental provisioning.

Females in populations with high mortality rates of eggs should have been selected to divide their egg mass by depositing smaller batches in each of several suitable locations. Distributing the eggs over many habitats may be seen as a form of spatial risk spreading, which should be a particularly useful strategy if the species breeds in highly unpredictable habitats (SCHENK et al., 2004). Spreading their eggs over a large number of habitats may therefore maximize reproductive success. Careful oviposition habitat selection increases offspring survival (SIVAJOTHY & HOOPER, 1995).

To avoid desiccation, the females of most odonate species could choose larger bodies of water or more open water. However, *S. infuscatum* eggs are desiccation resistant (WATANABE, 1996) and they diapause throughout the winter, during which time the soil of the rice paddy fields remains dry. Egg development occurs the following spring when the field is filled with enough water for rice planting. Thus there is a mechanism for suitable habitat selection for larval development

under seasonal changes in man-made water supplies for the cultivation of rice plants. The life history of *S. infuscatum* is tightly linked to the water management of the rice crop. Thus, if the race of rice cultured is changed, the corresponding water regime for the new race will be different from that of the old race, increasing the risk of non-suitable water habitat for the dragonfly larvae. Therefore, the status of *S. infuscatum* populations in Japan is very vulnerable among *Sympetrum* species, due to oviposition behaviour.

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REFERENCES

- BUSKIRK, R.E. & K.J. SHERMAN, 1984. The influence of larval ecology on oviposition and mating strategies in dragonflies. *Fla Ent.* 68: 39-51.
- CORBET, P.S., 1999. *Dragonflies: behavior and ecology of Odonata*. Cornell Univ. Press, New York.
- FINCKE, O.M., 1992. Consequences of larval ecology for territoriality and reproductive success of a Neotropical damselfly. *Ecology* 73: 449-462.
- HORVATH, G., 1995. Reflection-polarization patterns at flat water surfaces and their relevance for insect polarization vision. *J. theor. Biol.* 175: 27-37.
- HORVATH, G., P. MALIK, G. KRISKA & H. WILDERMUTH, 2007. Ecological traps for dragonflies in a cemetery: the attraction of *Sympetrum* species (Odonata: Libellulidae) by horizontally polarizing black gravestones. *Freshw. Biol.* 52: 1700-1709.
- KOSUGI, T., 2000. Oviposition of *Sympetrum* frequens onto an iron plate. *Insectarium* 37:187. – [Jap.]
- LAUGHLIN, S.B., 1976. The sensitivities of dragonfly photoreceptors and the voltage gain of transduction. *J. comp. Physiol.* 111: 221-247.
- MEINERZHAGEN, I.A., R. MENZEL & G. KAHLE, 1983. The identification of spectral receptor types in the retina and lamina of the dragonfly *Sympetrum rubicundulum*. *J. comp. Physiol.* 151: 295-310.
- MICHIELS, N.K. & A.A. DHONDT, 1990. Costs and benefits associated with oviposition site selection in the dragonfly *Sympetrum danae* (Odonata: Libellulidae). *Anim. Behav.* 40: 668-678.
- MIZUTA, K., 1978. Ovipositing strategy in *Sympetrum* species. *Insectarium* 15: 104-109. – [Jap.]
- MUTO, A., 1981. Oviposition behaviour of *Pantala flavescens* onto a roof of vehicle. *Nature & Insects* 16(14): 18. – [Jap.]
- SCHENK, K., F. SUHLING & A. MARTENS, 2004. Egg distribution, mate-guarding intensity and offspring characteristics in dragonflies (Odonata). *Anim. Behav.* 68: 599-606.
- SCHWIND, R., 1991. Polarization vision in water insects and insects living on a moist substrate. *J. comp. Physiol. (A)* 169: 531-540.
- SILSBY, J., 2001. *Dragonflies of the World*. The Natural History Museum. CSIRO Pub. Oxford.
- SIVA-JOTHY, M.T. & R.E. HOOPER, 1995. The disposition and genetic diversity of stored sperm in females of the damselfly *Calopteryx splendens xanthostoma* (Charpentier). *Proc. R. Soc. Lond. (B)* 259: 313-318.
- WATANABE, M., H. MATSUOKA, K. SUSAKI & M. TAGUCHI, 2005. Thoracic temperature in *Sympetrum infuscatum* (Selys) in relation to habitat and activity (Anisoptera: Libellulidae). *Odonatologica* 34: 271-283.

- WATANABE, M., H. MATSUOKA & M. TAGUCHI, 2004. Habitat selection and population parameters of *Sympetrum infuscatum* (Selys) during sexually mature stages in a cool temperate zone of Japan (Anisoptera: Libellulidae). *Odonatologica* 33: 169-179.
- WATANABE, M. & M. TAGUCHI, 1988. Community structure of coexisting *Sympetrum* species in the central Japanese paddy fields in autumn (Anisoptera: Libellulidae). *Odonatologica* 17: 249-262.
- WATANABE, Y., 1996. Embryonic development and early instar larvae of *Sympetrum*. *Nature & Insects* 31(8): 13-17. — [Jap.]
- WATSON, J.A.L., 1992. Oviposition by exophytic dragonflies on vehicles. *Not. odonatol.* 3: 155-156.
- WILDERMUTH, H., 1998. Dragonflies recognize the water of rendezvous and oviposition sites by horizontally polarized light: a behavioural field test. *Naturwissenschaften* 85: 297-302.
- WILDERMUTH, H. & G. HORVATH, 2005. Visual deception of a male *Libellula depressa* by the shiny surface of a parked car (Odonata: Libellulidae). *Int. J. Odonatol.* 8: 97-105.

**MULTI-LEVELS, MULTI-SCALES AND MULTI-FUNCTIONS
IN THE FINE STRUCTURE OF THE WING VEINS
IN THE DRAGONFLY *PANTALA FLAVESCENS* (FABRICIUS)
(ANISOPTERA: LIBELLULIDAE)**

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The internal fine structure of the wing veins is explored and the relationships between the structures and the functions of dragonfly wing veins are revealed. SEM photographs of the cross-sections of dragonfly wing veins have shown that: (a) the micro/nano structures vary along the axis of a vein, i.e. different cross-sections have different micro/nano structures. – (b) In a given cross-section, the micro/nano structures are at multi-levels and multi-scales. – (c) At a large scale, the structures of the veins are of diversities and disorders. The larger the size scale, the more complicated the structures and the higher are the diversities and disorders. The smaller the size scale, the simpler are the structures, and the higher are the unifications and orders. – (d) At nano scale, we may induce a unified assembling mode for the vein's structures, i.e. "nano fibres → nano layers (or nano bunches)". – (e) Both the mechanical and the biological functions of the micro/nano structures of the veins are optimized.

INTRODUCTION

In recent years, many researchers have studied systematically the structures and functions of dragonfly wings (BRACKENBURY, 1992; SONG et al., 2007; SUN, 2005; WOOTTON, 1991, 1992; WOOTTON et al., 2003; WANG et al., 2008). We have also made some progress. We focused on the outer surfaces of dragonfly wing veins (ZHAO et al., 2010a), and described randomly distributed wave-like ripples about 500~700 nm high and with distances between neighbour-

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ing peaks around 1~3 μm . In addition, sharp spikes with a height of 20~80 μm were observed, on the surface of which were regular straight waves with a height of 600~800 nm and distances between neighbouring peaks about 2~3 μm . We explored the cross-section of the pterostigma of dragonfly (ZHAO et al., 2010b) and found a vessel-like structure with curved walls, and also composite constructions of nano-fibre reinforced multiple layers. We focused on the vein/membrane/spike junctions (ZHAO et al., 2011) where the smooth transition modes and global package assembly modes were discovered. In this paper, we will concentrate on the internal fine structures of dragonfly wing veins.

Researchers have pointed out that dragonfly wing veins are of sandwich-tube structures (WANG et al., 2008). This paper will further confirm the following: (a) Dragonfly wing veins are diversified tube-like structures, and the sandwich-tube structure is just one type. – (b) Inside the sandwich-tube structure, there are extremely fine multi-level fine structures. – (c) Along with the changes of load-carrying functions and transporting functions, the structures of a dragonfly wing vein changes along its axis. – (d) At the nano scale, the structures of dragonfly wing veins obey unified assembly modes.

MATERIAL AND METHODS

A right forewing of *Pantala flavescens* was used (Fig. 1). The forewing was pre-fixed in 2.5% glutaraldehyde at 4°C for 3 hours, rinsed in 0.1mol/L phosphate buffer, then fixed in 1% Osmium tetroxide for 1 hour and rinsed several times in 0.1mol/L phosphate. It was then placed successively into 30%, 50%, 60%, 70%, 80%, 90% (two changes), 90% ethanol mixed with 90% acetone and 100% acetone, with 15min in each solution. After dehydration the sample was embedded in epoxy resin and cured

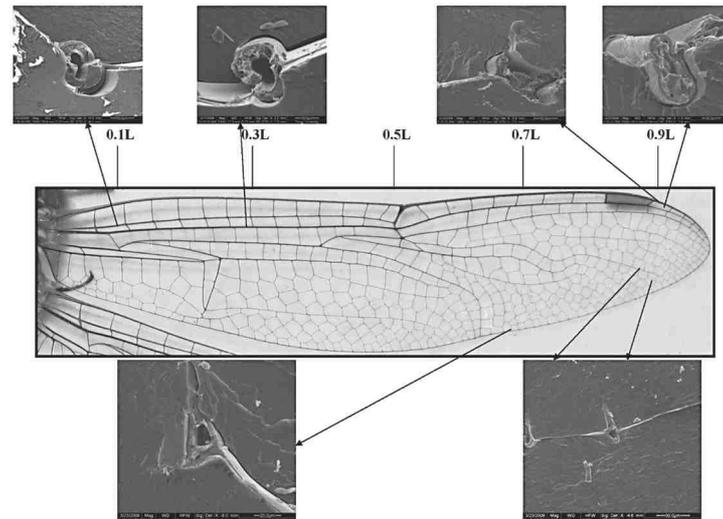


Fig. 1. The “map” for the measured cross-section of the veins in the right forewing of *Pantala flavescens*.

at room temperature for 24 hours. The sample was then immersed in liquid nitrogen for 1~2 min, taken out and broken to obtain brittle fracture cross-sections of the wing. Finally, the broken pieces of wing were coated with gold about 6nm thick and observed using an *FEG-ESEM*.

The length of the right forewing was $L \approx 4.2$ cm. For references we labeled the scale marks, $0.1L$, $0.3L$, $0.5L$, $0.7L$ and $0.9L$. For comparisons we observed the cross-sections of different veins. The detailed “map” for observed locations is shown in Figure 1.

GENERALITIES AND PARTICULARITIES IN THE VEIN STRUCTURES

There are very large differences in internal structures of different cross-sections of the veins. Since structure determines function. We analyzed the structures of different cross-sections together with the functions of the wing veins. For comparisons, the wing is divided into four districts, i.e. basal, the leading edge, trailing edge and tip district.

UNIFICATION IN THE TUBE-LIKE VEINS

The longitudinal and cross veins in the leading and trailing edges of the wing are all tube-like structures. The tube-like structures of dragonfly wing veins have been reported many years ago (WOOTTON, 1991) and will not be further explained in this paper. Here we will analyze the relationships between structure and function.

From the viewpoint of engineering mechanics, the tube-like structure of the veins is an optimized one. Thus the veins mainly bear bending deformations and torsion deformations. Although the materials of the veins are not uniform and isotropic, for simplification we only consider a uniform and isotropic tube-like bar. Suppose this tube-like bar is loaded by bending momentum M_y and torsion momentum M_x on a cross-section (Fig. 2). Then the normal stress σ and shear stress τ on the cross-section of the bar may be written respectively as formula (1) and (2):

$$\sigma(z) = \frac{M_y z}{I_z}, \quad I_z = \int_A y^2 dA \quad (1)$$

$$\tau(\rho) = \frac{M_x \rho}{I_p}, \quad I_p = \int_A \rho^2 dA, \quad \rho^2 = y^2 + z^2 \quad (2)$$

Here point O is the centre of the tube's cross-section, y and z are respectively the principle axes through the centre. I_z is the inertia momentum of the cross-section around the z axis. I_p is the polar inertia momentum of the cross-section around the centre point O . Obviously, the nearer the point is to the centre (i.e. the

smaller is $|z|$ or ρ), the lower is the stress level. The further the point is from the centre (i.e. the larger is $|z|$ or ρ), the higher is the stress level. Therefore, the maximum bending stress σ_{\max} and the maximum torsion stress τ_{\max} all occur at the points of the outer edge with $|z|_{\max}$ and ρ_{\max} . The tube with a central hole coincides with the stress distributions.

Because the stress level around the centre is low,

the hole around the central area may not affect the load-carrying capacity of the vein. On the contrary, the tube with a central hole may reduce the weight of the vein. This advantage can also be understood as follows: For a fixed material weight (or given cross-section area), the inertia momentum I_z and the polar inertia momentum I_p will be raised if the materials inside the lower-stress region near the centre are removed to the higher-stress region far away from the centre. Once I_z and I_p are increased, the normal stress σ and shear stress τ may be reduced, and the utilization rate of the materials and the load-carrying capacity of the bar may be enhanced. The above explanations are aimed at the uniform and isotropic bar, but they are also valid for the non-uniform and anisotropic tube-like veins.

From the viewpoint of biology, the tube-like veins form the unique transportation system (ARNOLD, 1964). The central holes of the veins can realise important physiological functions: They are both the transportation paths for blood flow in the wing and the main transportation passages for nerves signals.

The above structures and functions of the dragonfly wing veins provide references for the bionic designs. In aircrafts, the load-carrying systems, transportation systems and controlling systems are usually very complicated, and their functions are usually independent. In comparison with aircrafts, dragonflies “choose” the more simplified, more synthesized and more integrated schemes.

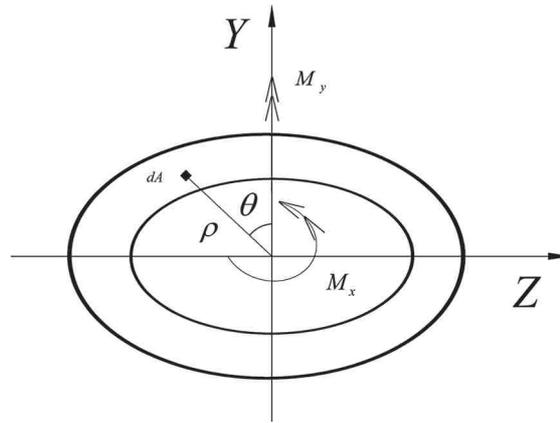


Fig. 2. The cross-section of a tube loaded by bending and torsion momentums.

DIFFERENT SHAPES

The microscopic photos in Figure 1 are magnified and arranged in counter clock sequence in Figures 3-8. Although all the veins are tube-like structures, there are very large differences between them.

First, their geometric shapes are different. Thus the vein at the trailing edge is a

tube with curved-triangle cross-section, i.e. its inner contour is a convex curved-triangle and its outer contour is a concave curved-triangle (Fig. 3). The cross-section of the longitudinal vein at the tip of the wing looks like a dumbbell, i.e. this longitudinal vein is a dumbbell-shaped tube (Fig. 5). The inner and outer contours of the cross-section of the longitudinal vein near the leading edge at the tip of the wing are formed by four extremely curved lines, i.e. this longitudinal vein is a curved-quadrangle-shaped tube (Fig. 6). The cross-section of the Radius looks like a pear, i.e. this Radius is a pear-shaped tube (Fig. 7). In Figure 4, the vein is indeed of tube-like shape but the existence of the sharp spike (ZHAO, et al., 2010a) enhances the complicity of the local shapes: the two neighboring veins are both cylindrical tubes and the spikes on the two veins are all conical tubes (ZHAO, et al., 2011). Thus the cylindrical tube and the conical tube together form a “T-type” or tee joint tube.

In general, the nearer is the vein is to the wing edge, the more complex is its geometric shape. In Figure 3, the contour of the curved-triangle-shaped tube bends as a bow. In Figures 5 and 6, the contours of the dumbbell-shaped tube and the curved-quadrangle-shaped tube raise as surging waves. Why are the outer shapes of the veins along the wing edge so complicated? After a few hundred million years' evolutions, every part of the dragonfly should be optimized. Veins with strange shapes realize a specific function which may be closely related to the flow control at the edge or to the air dynamics optimizations of the wing.

When a dragonfly flies, the air current flows into or out off the wing from the leading edge, trailing edge and the tip. When the air current flows out off the edges of the wing, it will feel forces produced by the contour of the edge and change the direction of flow. For example, in Figure 3 the contour of the concave curved-triangle forms a curved surface that acts as a diversion. Thus, when the

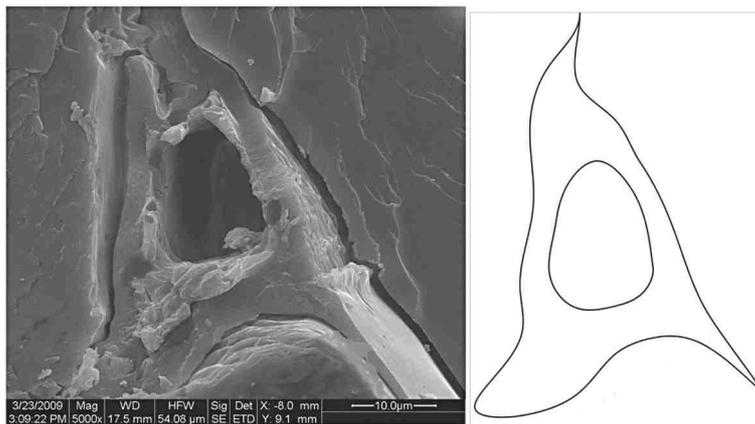


Fig. 3. *Pantala flavescens*: cross-section of the longitudinal vein at the trailing edge of the wing marked 0.7L and the skeleton map of the adult.

air stream on the bottom wing surface reaches the trailing edge vein, its direction of flow will be drastically varied by the diversion curved surface. This variation

in stream direction may lead to a reaction force. This reaction force may increase the lift of the wing. Thus the diversion curved surface is able to enhance the lift force on the wing. In an airplane, such an enhancement mechanism for lift force is realized by the aileron (Fig. 9). Therefore, we may say that the diversion curved surface and the aileron are of identical functions in strengthening lift force.

Similarly, in Figures 5 and 6, the contours of the veins around the wing tip are also diversion curved surfaces. When the longitudinal stream on or parallel to the bottom surface of the wing reaches the region of the tip, its parallel direction will be varied vertically downwards by the diversion curved surfaces, and the lift force will be increased. Besides, the downward stream at the tip district may efficiently restrain the “washing-down effect”. In an airplane, the “washing-down effect” is controlled by the tiny wing (Fig. 9) fixed at the tip of the wing. Hence we may say that the diversion curved surfaces and the tiny wings are of identical function in eliminating “washing-down effect”.

In summary, the complicated geometric shapes of the veins along the wing edges may either enhance the lift force or eliminate the “washing-down effect”.

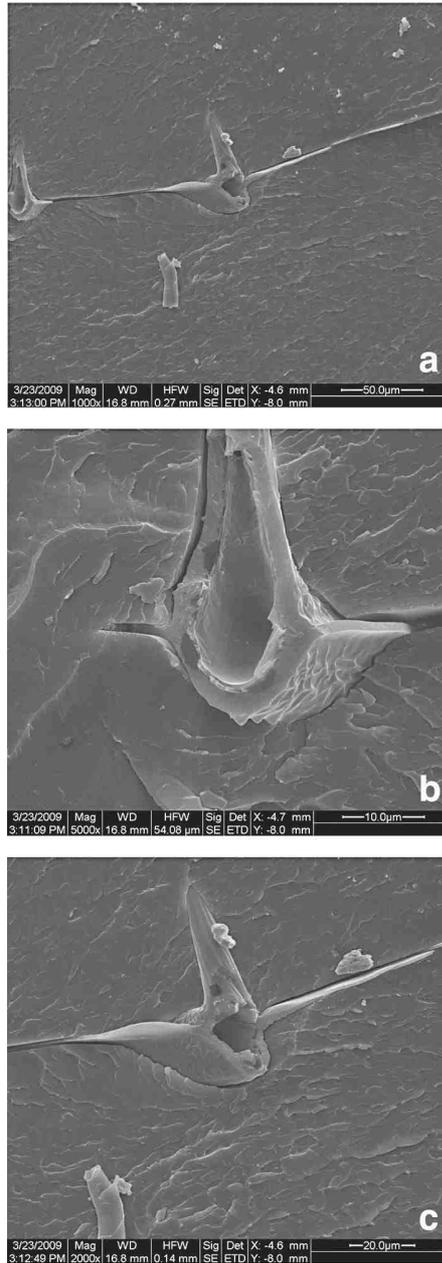


Fig. 4. *Pantala flavescens*: (a) cross-sections of the two neighbouring veins and spikes near the wing tip marked $0.9L$; – (b) cross-sections in the vein and spike at the left side of Fig. 4a; – (c) same, at the right side.

DIFFERENT SIZES

The geometric sizes are different. In different wing regions, the characteristic diameters of the veins are different: In the region of the base and of the leading edge the veins are thick. In Figure 7a, the diameter of the radius is about 100 μ m. In the wing tip and trailing edge regions the veins are thin. In Figure 4b, the diameter of the vein around the tip and trailing edge is only about 10 μ m. The differences in sizes are very easy to understand: The longitudinal veins of the dragonfly wing near the leading edge act as the principle beams, just as the principle beam of an airplane wing. These longitudinal veins have to bear most of the external loads and should be strong enough. If we pay attention to the load paths, we may find that all the lift and thrust acting on the wing will be transmitted to the body of the dragonfly through the base of the veins. Hence the veins around the basal region must be thick enough. On the contrary, around the trailing edge and in the area the wing tip the main functions of the veins are to support the membranes. Because the loads carried in such regions are small, the veins are thin. Under the precondition for assuring strength, thinner veins may reduce effectively the weight of the wing.

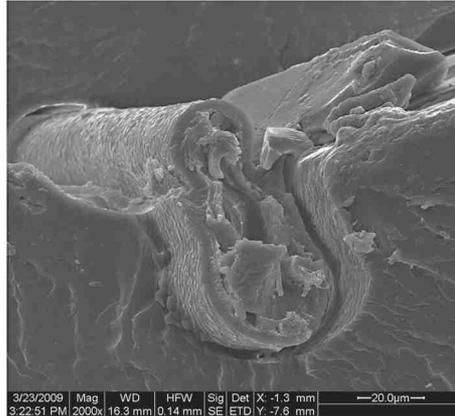


Fig. 5. *Pantala flavescens*: cross-section of the radius near the wing tip marked 0.9L.

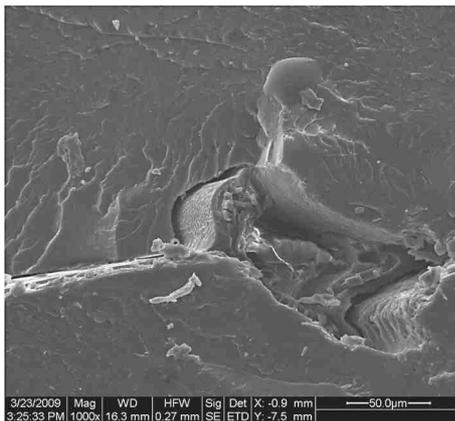


Fig. 6. *Pantala flavescens*: cross-section of the costa at the tip marked 0.9L.

DIFFERENT STRUCTURES:
BILAYER TUBES AND
MULTILAYER TUBES

The micro/nano structures are different. In Figures 3~7, all the cross-sections of the veins are of multi-level structures. However, in different regions the multi-level structures are also different: The thicker the veins, the more complicated are the internal structures; the thinner the veins, the simpler are the internal structures.

In the regions of the trailing edge and the wing tip, where the loads are small, the thin veins have simpler structures: they are all bilayer tubes with both an inner layer and an outer layer (Fig. 3). Although the external shape of the “T-type” vein/spike joint is complex, the internal construction is also a bilayer structure (Fig. 4): the vein is a bilayer cylindrical tube, while the spike is a bilayer conic tube. Because the vein is packaged by membranes (ZHAO et al., 2011), the outer layers of the bilayer tubes are all parts of the membranes. In Figures 3 and 4, the outer layer is thicker (about 4~6 μm). The inner layer is extremely thin (about 1~2 μm) but may also be laminated; In Figure 4a the inner layer is divided into two sub-layers.

In the basal and leading edge regions where the loads are high, the cross-sections of the thick veins are not bi-

layer structures but are multi-layer structures or multi-layer tubes (Figs 5-8). Cross-sections of the veins at the leading edge show the sandwich features (this result coincides with that in WANG et al. (2008), i.e. a middle layer (Figs 5, 6) 5~10 μm thick between the outer and inner layers. In Figure 7, the constructions of the micro/nano structures inside the sandwich middle layer of the radius are revealed. Because relative dislocation occurs during brittle fracture of the radius, the left-upper part and the right-lower part of Figure 7 belong to two different fractured sections. The right-lower section is nearer to the camera lens and shows the sandwich feature. The left-upper section is further from the camera lens and shows cleavage (Fig. 7a). If the cleavage surface is magnified (Fig. 7b), the nano bunches (about 100~200 nm diameters) and nano layers (about 100~200 nm thickness) formed by nano fibres (about 30 nm diameters) are displayed. The bunches seem to be helical and the direction of the helix axis is near to the direction of

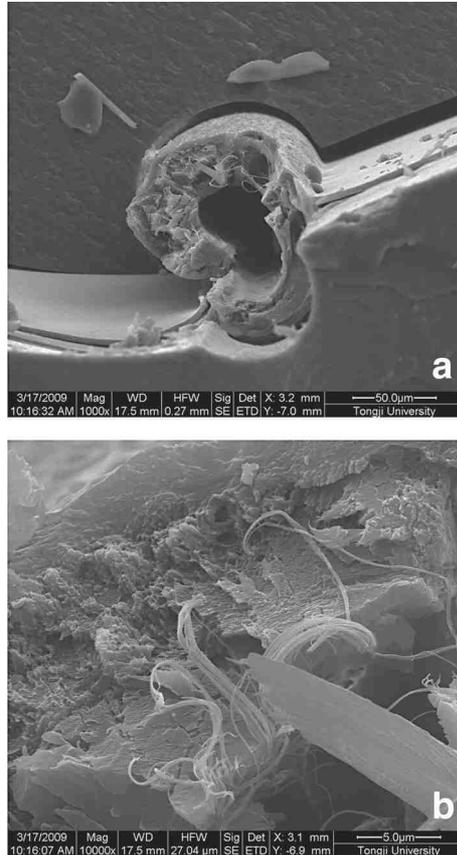


Fig. 7. *Pantala flavescens*: (a) fracture surface of the radius marked 0.3L; – (b) magnified photograph of the left-upper fracture surface in Fig. 7a.

the vein axis. Thus the sandwich middle layer of the radius is made of composite materials reinforced by fibres.

The structures of the subcosta in the basal region are extremely complicated (Fig. 8) and will be discussed independently in the following sections.

THE MULTI-LEVEL AND MULTI-SCALE STRUCTURES IN THE SUBCOSTA

From Figure 8, we can see that the cross-section of the subcosta in the basal region is an elliptic multi-layer tube. Its outer diameter is about 100 μm . The length of the longer axis is about 50 μm and the length of the shorter axis is about 30 μm . In Figure 8a, relative dislocation can be seen at the membrane plane when the subcosta is fractured, i.e. the fracture of the vein occurs in two different sections. The upper fracture section is further from the camera lens than the lower fracture section.

THE UPPER FRACTURE SECTION

From Figure 8b, the upper fracture section can be seen to be a multi-level or multi-layer structure with four layers: i.e. inner, middle, transition and outer layers. The outer layer is part of the membranes (ZHAO et al., 2010b), the transition layer is about 6 μm thick and its fracture

Fig. 8. *Pantala flavescens*: (a) brittle fracture sections of the subcosta marked 0.1L; – (b) locally magnified photograph of the upper section in Fig. 8a; – (c) same of the lower fracture section in Fig. 8a.





Fig. 9. The ailerons and tiny wings at the wing-tip of an airplane. – [http://baike.baidu.com/albums/85119.html#0\\$43e6c733717dcd71ac4b5f3f](http://baike.baidu.com/albums/85119.html#0$43e6c733717dcd71ac4b5f3f).

surface shows honeycomb-like morphology.

The inner layer is an elliptical laminate composite shell (Fig. 8b) with six sub-layers. The thickness of each sub-layer is about $1.2\ \mu\text{m}$. The six sub-layers look like six coaxial tubes connected closely together. Along the circumference direction, every coaxial tube is not a “seamless tube” but is an “assemble tube” connected by “thin shell” and “thin plate”.

The “thin shell” and “thin plate” are formed by the continuous stacking of extremely thin nano layers, and every nano layer is the condensed compaction of parallel nano fibres. We believe that the inner layer is of such an assembling mode: parallel nano fibres \rightarrow nano layers \rightarrow micro sub-layer \rightarrow inner layer.

The thickness of the middle layer is about $11\ \mu\text{m}$. In Figure 8b, the cleavage surfaces of the middle layer are fanwise morphologies. Inside the fanwise morphologies there are fine nano structures: condensed nano fibres are compacted into nano layers and the nano layers are stacked into radiated fanwise morphologies. The nano fibres appear to twine around the axis of the vein along a helix surface, which leads to the fanwise morphologies in Figure 8b. Hence the middle layer may be of such an assembling mode: nano fibres \rightarrow nano layers \rightarrow helix stacking \rightarrow middle layer.

THE LOWER FRACTURE SECTION

A sandwich feature is shown in the lower fracture section (Fig. 8c). Among the three layers of the sandwich, the outer layer is $5\sim 8\ \mu\text{m}$ thick, the inner layer is extremely thin but the middle layer is much thicker. The structure of the middle layer is very regular and ordered and is very similar to the fanwise morphology shown in the Figure 8b: nano fibres are adhered into nano layers, and the nano layers twine around the vein axis along a helix surface. The layer-by-layer stacking of nano layers will lead to the fanwise constructions of the middle layer. We suggest that: if the distance of two neighboring cleavage surfaces is smaller than a few hundred nano metres along the vein axis, then the multi-layered cleavages will lead to the morphologies in Figure 8c.

It is noted that the distance between the upper and lower fracture sections is only about $20\ \mu\text{m}$ (Fig. 8a). Nevertheless, the structures of the two fracture sections show enormous differences both in micrometer scale and in nanometer scale.

It would be interesting to know how the vein structure changes between the two fracture sections. Do the structures change gradually or suddenly? We have no answers now, but we are sure that the structures and properties of the subcosta are changed both between the two fracture sections and along the whole vein axis.

UNIFIED ASSEMBLING MODE

The veins of the dragonfly wing are of “multiple characteristics”, i.e. multi-levels, multi-layers, multi-scales and multi-functions. These “multiple characteristics” lead to the complicity and diversity of the veins. Nevertheless, although variations in vein structures exist at the micrometre level, there are common aspects to the nanometre structures: Most of the micrometre structures are laminated by nano layers (or twined by nano bunches), and most nanometer layers (or nano bunches) are compacted by nano fibres. Therefore we may say that there is a unified assembling mode at the nanometre scale for dragonfly wing veins: compacted nano fibres → laminated nano layers (or twined nano fibres). In other words, the strategy for the dragonfly growing wing veins is “to meet all changes by remaining unchanged”, i.e. at the macro scale the structures may be infinite in variety, but at the nanometre scale the structures are invariant. Commonly speaking, the wing veins may be compared as a group of buildings. Although enormous differences among buildings may exist, the basic bricks for all buildings are identical. Identical bricks but different stacking sequences, will lead to different buildings with different functions.

Dragonfly wing veins give us such inspirations:

- (a) The larger the size scale, the more complicated and more divergent the structures. The diversity and complicity of the structures at large scales come from the diversity in external loads and the complicity in deformations of the veins, and also come from the synthesis and optimization in macro functions: On the one hand, the external loads acting on the wing change rapidly under complex flying conditions. Hence, at different moments both the stress is different and the deformation is different at the same point inside the vein. On the other hand, the veins need both optimal load-carrying function and optimal biological function. Different optimal functions have to be integrated optimally as a whole. To face complicated conditions for external loads and to meet strict conditions for optimal functions, the vein must be highly differentiated.
- (b) The smaller the size scales, the simpler and the more unified are the structures. The simplicity and the unification of the structures at small size scales come from the monotonicity of the dynamic self-assembling mode: The nanometre structures inside the dragonfly wing veins are all grown from the nonlinear dynamic, self-assembling of organic molecules. To assure the accuracy of the self-assembling and to reduce the error or mismatch in self-assembling, the varieties of organic molecules should be as few as possible, and the self-

- assembling mode should be as simple as possible.
- (c) The structures of the vein are simple at a small size scale and complicated at a large size scale. Hence, the processes of stacking and self-assembling from microscopic to macroscopic structures are also the processes from simplicity to complexity, from order to disorder, and from single function to multiple functions.

CONCLUSIONS

As the product of three hundred million years of evolution, the dragonfly wing vein is a unit of simplicity, complexity and optimization. The complexity of the structures at the large size scale is to meet the needs for the complicated survival conditions, whereas the simplicity of the structures at the small size scale is to meet the requirement for high-efficiency in dynamic self-assembling. Both the simplicity and the complexity in structures are to meet the needs for optimizations in mechanical and biological functions. The profound mysteries in the dragonfly wing veins provide valuable references for bionics of aircrafts with small size scales.

ACKNOWLEDGEMENTS

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REFERENCES

- ARNOLD, J.W., 1964. *Blood circulation in insect wings*. Ent. Soc. Canada, Ottawa.
- BRACKENBURY, J., 1992. *Insects in flight*. Blandford Press, London.
- SONG, F., K.W. XIAO, K. BAI & Y.L. BAI, 2007. Microstructure and nanomechanical properties of the wing membrane of dragonfly. *Mater. Sci. Eng. (A)* 457: 254-260.
- SUN, M., 2005. High-lift generation and power requirements of insect flight. *Fluid Dyn. Res.* 37: 21-39.
- WOOTTON, R.J., 1991. The functional morphology of the wings of dragonflies. *Adv. Odonatol.* 5: 153-169.
- WOOTTON, R.J., 1992. Functional morphology of insect wings. *Annu. Rev. Ent.* 37: 113-140.
- WOOTTON, R.J., R.C. HERBERT, P.G. YOUNG & K.E. EVANS, 2003. Approaches to the structural modeling of insect wings. *Phil. Trans. R. Soc. Lond. (B)* 358: 1577-1587.
- WANG, X.S., Y. LI & Y.F. SHI, 2008. Effects of sandwich microstructures on mechanical behaviors of dragonfly wing vein. *Compos. Sci. Technol.* 68: 186-192.
- ZHAO, H.X., Y.J. YIN & Z. ZHONG, 2010a. Micro and nano structures and morphologies on the wing veins of dragonflies. *Chin. Sci. Bull.* 55: 1993-1995.
- ZHAO, H.X., Y.J. YIN & Z. ZHONG, 2010b. Nano fibrous multilayered composites in pterostigma of dragonfly. *Chin. Sci. Bull.* 55: 1856-1858. – [Chin.]
- ZHAO, H.X., Y.J. YIN & Z. ZHONG, 2011. Assembly modes of dragonfly wings. *Microsc. Res. Tech.* 74(12): 1134-1138.

SHORT COMMUNICATION

DESCRIPTION OF FEMALE OF *NIHONOGOMPHUS SCHORRI* DO & KARUBE FROM HUU LIEN NATURE RESERVE, LANG SON PROVINCE, NORTH VIETNAM (ANISOPTERA: GOMPHIDAE)

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The ♀, collected from the type locality of the sp., Huu Lien Nature Reserve, Lang Son Province, North Vietnam, is described and illustrated in detail.

INTRODUCTION

The species *Nihonogomphus schorri* was described by DO & KARUBE (2011) based on male specimens collected from Huu Lien Nature Reserve, Lang Son Province, North Vietnam. The original description included also a brief characterization of the female sex based on an available photograph. Here we provide a detailed description of the female, based on a single specimen collected in the same reserve in June 2011.

N. schorri is close to *N. bequaerti* Chao, which was described on a ♂ specimen from Fujian, China (CHAO, 1954).

DESCRIPTION OF FEMALE

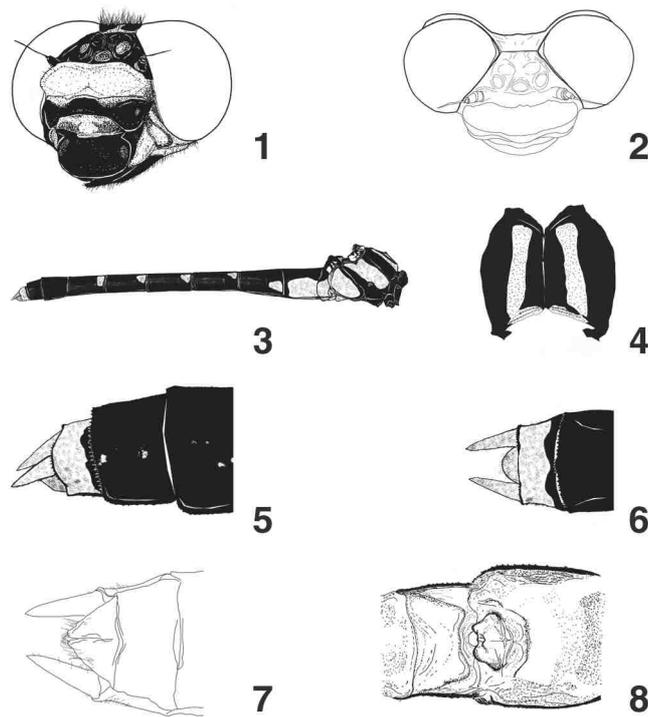
Figures 1-10

M a t e r i a l. – ♀ Vietnam, Lang Son Province, Huu Lien Nature Reserve, Lan Ti Community, alt. 250 m, 21-VI-2010, Do Manh Cuong leg.; deposited in Entomology and Zoology Collection, Military Institute of Hygiene and Epidemiology, Hanoi, Vietnam.

H e a d. – Black with greenish marking, occiput black with a fade marking at middle line which separates the occiput into two black areas, the middle fade line connects with other fade line parallel with the postocellar suture. Vertex wholly black with two domed prominences above lateral ocelli. Frons protrusive and wholly greenish, the greenish colour passes over epistomal suture and over upper margin of postclypeus which is shining black. Anteclypeus greenish with darker areas at lower lateral sides. Labrum shining black. Haft of mandible from base yellow greenish, apical part black. Genae yellowish white. (Figs 1-2).

T h o r a x. – Thorax coloured similarly as in male. Prothorax entirely black. Mesepisternum black with broad upside-down 7-shaped greenish markings. Dorsal carina with yellow spot in anterior part. Sides of pterothorax black with two broad greenish bands, the upper band covering parts of mesepimeron and metepisternum, the lower band covering most of metepimeron (Figs 3-4). Legs entirely shining black.

Wings hyaline. There are 19 antenodal cross veins in Fw and 14 in Hw; 14 post-

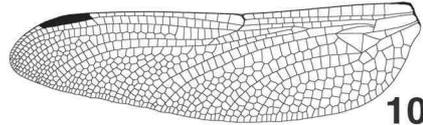
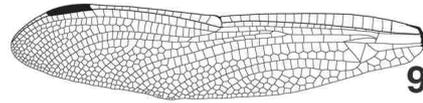


Figs 1-8. *Nihonogomphus schorri*, female: (1) head; – (2) same, dorsal view; – (3) body, lateral view; – (4) synthorax, dorsal view; – (5) cerci, lateral view; – (6) same, dorsal view; – (7) same, ventral view; – (8) subgenital plate.

nodal cross veins in Fw and Hw. Pterostigma covers 6-7 underlying cells (Figs 9-10).

A b d o m e n. – In dorsal view, abdomen black with markings as follows: segments 1-2 with middorsal greenish stripe that continues to base of S3; S4-7 with pair of dorsolateral yellowish dots; S8-9 entirely black; S10 nearly whole yellowish except a black line basally. Cerci entirely yellowish. Subgenital plate trapezium generally, posterior margin with a middle concave to form two apical round lobes (Figs 3, 6-8).

M e a s u r e m e n t s (mm). – Hindwing: 32.5; abdomen: 47 (including cerci).



Figs 9-10. *Nihonogomphus schorri*, female: (9) forewing; – (10) hindwing.

DISCUSSION

The body markings of the specimen studied match very well to the female specimen photographed (DO & KARUBE, 2011, fig. 16) by the first author in the same locality in 2009. The head and body markings are similar to the male of *N. schorri*. Whereas in the male, the front legs are black with large yellowish-green marking along outer side of femur, it is whole black in the female. Since the female of the closely related species, *N. bequaerti*, is unknown, it is not possible to compare. Further studies are needed to determine the other characteristics of the species such as larvae, aquatic life, distribution, conservation and status of populations.

ACKNOWLEDGMENTS

The first author is most thankful to the International Dragonfly Fund (IDF) for the supporting of the field works in 2010 and 2011 and thanks MATTI HÄMÄLÄINEN for support in the field trip to Huu Lien in 2010. We thank Matti Hamalainen for help on revising and promoting the manuscript.

REFERENCES

- CHAO, H-f., 1954. Classification of Chinese dragonflies of the family Gomphidae (Odonata), 4. *Acta ent. sin.* 4(4): 399-426. – [Chin., with Engl. s.]
 DO, M.C. & H. KARUBE, 2011. *Nihonogomphus schorri* sp. nov. from Huu Lien Nature Reserve, Lang Son Province, Vietnam (Odonata: Gomphidae). *Zootaxa* 2831: 63-68.

ODONATOLOGICAL ABSTRACTS

2007

- (18853) BECHLY, G., 2007. [The Crato fossil beds in Brazil]. Odonata: damselflies and dragonflies. *In*: D.M. Martill, G. Bechly & R.F. Loveridge, [Eds], *The Crato fossil beds in Brazil: window into an ancient world*, pp. 184-222, pls 9-10 & bibl. references excl. – (Staat. Mus. Naturk., Rosenstein 1, D-70191 Stuttgart).
It includes the descriptions of the following new taxa: *Euarchistigma marialuiseae* sp. n., *Cratostenophlebia schwickerti* gen. n., sp. n., *Eotanypterix paradoxa* gen. n., sp. n., *Cordulagomphus winkelhoferi* sp. n., *C. hanneloreae* sp. n. and *C. (Procordulagomphus) michaeli* sp. n. 2 uncertain new spp. in Parahemiphebia and Araripegomphus are diagnosed and commented upon but not named.
- (18854) BESCHOVSKI, V. & M. MARINOV, 2007. Fauna, ecology and zoogeography of dragonflies (Insecta: Odonata) of Bulgaria. *In*: V. Fet & A. Popov, [Eds], *Biogeography and ecology of Bulgaria*, pp. 199-231, Springer, Dordrecht. – (First Author: Inst. Zool., Bulg. Acad. Sci., Tsar Osvoboditel Blvd 1, BG-1000 Sofia).
68 spp. are known from Bulgaria and are classified as rheophilous and limnophilous. Adaptations to both larval habitat complexes are discussed. Biogeographic characteristics are outlined on the gen. and sp. levels, and the vertical and horizontal distribution is stated. 7 phenological groups are established and their habitats are divided into 12 types.
- (18855) BUDEN, D.W. & D.R. PAULSON, 2007. Odonata of Yap, western Caroline Islands, Micronesia. *Pacif. Sci.* 61(2): 267-277. – (First Author: Dept Nat. Sci. & Mathem., Coll. Micronesia, P.O. Box 159, Kolonia, Pohnpei-96941, F.S. Micronesia). 15 recorded spp. are listed and commented upon; none is endemic to Yap.
- (18856) FEULNER, G.R., R.W. REIMER & R.J. HORNBY, 2007. An updated illustrated checklist of dragonflies and damselflies of the U[nited]A[rab]E[mirates]. *Tribulus* 17: 37-62. – (First Author: P.O. Box 31045, Dubai, UAE).
Ceriagrion glabrum, *Pseudagrion decorum*, *Ischnura senegalensis*, *Orthetrum rasonneti*, *Crocothemis sanguinolenta* and *Sympetrum fonscolombii* are added to the checklist as published by G. Giles (1998, *Tribulus* 8/2: 9-15). – For another addition and for the correction in identification of some photographs, see *OA* 18904.
- (18857) HOLUŠA, O., 2007. The results of the faunistic research of dragonflies (Odonata) in the Podyjí National Park and in several localities in the surroundings. *Thayensia* 7: 239-247. (Czech, with Engl. s.). – (Bruzovská 420, CZ-738-01 Frýdek-Místek). 33 spp. are listed from 19 localities, incl. *Coenagrion scitulum*, *Anax parthenope*, *Crocothemis erythraea* and *Leucorrhinia pectoralis*; – Czech Republic.
- (18858) HOLUŠA, O. & P. JEZIORSKI, 2007. Collection of dragonflies (Insecta: Odonata) in the Ostravian Museum (Czech Republic). *Práce Stud. Muz. Beskyd (Přir. Vědy)* 19: 143-150. (Czech, with Engl. s.). – (Second Author: Na Bělidle 1, CZ-735-64 Havířov-Suchá).
An annotated list of 39 spp. from the Czech Republic, Croatia, Hungary and Macedonia.
- (18859) LADET, A. & C. BOUVET, [Eds], 2007. *Inventaire des odonates et suivi des échanges sur les*

- tourbières du Plateau de Montselgues*. Féd. Rhône-Alpes Prot. Nature, FRAPNA Ardèche, St Etienne de Fontbellon. 50 pp. – (Publishers: FRAPNA, La Village, F-07200 St. Etienne de Fontbellon).
26 spp. are listed and their occurrence on the Plateau de Montselgues (Montselgues & Malarce-sur-la-thines, dépt Ardèche, France) is outlined.
- (18860) LEMELIN, R.H., 2007. Understanding dragon-hunters and Odonata interactions in protected areas. *Proc. 2007 George Wright Soc. Conf.*, Hancock, MI, pp. 132-136. – (Sch. Outdoor Recreation, Parks & Tourism, Lakehead Univ., Thunder Bay, ON, P7B 5E1, CA).
As highlighted by a study conducted on wildlife tourists visiting S African protected areas, managers were often “fairly surprised to learn that tourists had indicated an interest in being shown the invertebrate fauna”. A far more effective translation of the diverse values of invertebrates and their environment will be needed. Odon. are excellent subjects for nature interpretation programs and public education. The interviews with numerous amateur odonatologists are briefly summarised.
- (18861) LOIOLA, G.R., A.F. VAN DE KOKEN, K.S. FURIERI & P. DE MARCO, Jr, 2007. Aspectos populacionais de fêmeas de *Heteragrion aurantiacum* (Odonata: Megapodagrionidae) e ocorrência de *Heteragrion* spp. no centro e norte do Espírito Santo. *Anais 8 Congr. Ecol. Brasil*, 2 pp. (Port.). – (Last Author: Lab. Ecol. Teórica, Depto Biol. Geral, Univ. Fed. Goiás, BR-74001-970 Gojânia, GO).
The size and density of ♀ *H. aurantiacum* populations in Reserva Biológica de Córrego Grande (Espírito Santo state, Brazil) were estimated at hardly 2.05 ind./h (31 individuals sighted). The ♀♀ of this sp. are spending long periods resting away from water, therefore they are difficult to detect.
- (18862) NOVELO GUTIÉRREZ, R. & P.E.A. EGUIA LIS, [Eds], 2007. *Simposio internacional Entomología Acuática Mexicana: estado actual de conocimiento y aplicación*. Inst. Mex. Tecnol. Agua, Mexico. 104 pp. (Mostly Span., with Engl. s's).
[Odonatol. papers]: *Novelo Gutiérrez, R.*: El estudio de los odonatos (Insecta: Odonata) en México: enfoques y perspectivas (pp. 9-23); – *Pérez Munguía, R.M.*: Uso de los macroinvertebrados acuáticos en el monitoreo ambiental de ríos y arroyos (pp. 63-77).
- (18863) PROKOP, J., T. PŘIKRYL, O. DOSTAL & A. NEL, 2007. *Oligaeschna kvaceki* sp. n., a new fossil dragonfly (Odonata: Aeshnidae) from the Middle Oligocene sediments of northern Moravia (western Carpathians). *Geologica carpathica* 58(2): 181-184. – (First Author: Dept Zool., Charles Univ., Viničná 7, CZ-128-44 Praha-2).
The new sp. is described, illustrated and compared with the closely related spp. The present record documents a rather broad distribution and probably also high *Oligaeschna* abundance in Eurasia during the Oligocene and Miocene.
- (18864) VAN DE KOKEN, A.F., G.R. LOIOLA, K.S. FURIERI & P. DE MARCO, Jr, 2007. Ocorrência e aspectos populacionais de *Telagrion* spp. (Odonata: Coenagrionidae) no norte do Espírito Santo e sul da Bahia. *Anais 8 Congr. Ecol. Brasil*, 2 pp. (Port.). – (Last Author: Lab. Ecol. Teórica, Depto Biol. Geral, Univ. Fed. Goiás, BR-74001-970 Gojânia, GO).
The distribution, habitats and habits of *T. cornicauda*, *T. longum* and *T. mourei* in N Espírito Santo and S Bahia (Brazil) are briefly outlined.
- (18865) VAN GOSSUM, H., K. BEIRINCKX, M.R. FORBES & T.N. SHERRATT, 2007. Reproductive interference between *Nehalennia* damselfly species. *Ecoscience* 14(1): 1-7. (With Fr. s.). – (First Author: Evol. Biol. Gr., Dept Biol., Univ. Antwerp, Groenenborgerlaan 171, B-2020 Antwerpen).
The hypotheses that reproductive interference between 2 congeneric Zygoptera spp. influences their local population densities and the ♀ morph ratios in one of these was tested. *N. irene* has 2 ♀ types (andromorph and gynomorph), whereas *N. gracilis* exhibits only one ♀ type. Andromorphic *N. irene* ♀♀ not only resemble conspecific ♂♂ in body coloration, but also resemble heterospecific ♀♀ of *N. gracilis*. It was predicted ♂ *N. irene* to be most attracted to gynomorphs of *N. irene* and ♂ *N. gracilis* to be least attracted to them. Further, if *N. gracilis* ♂♂ harass andromorphic *N. irene* ♀♀ excessively, then they may reduce andromorph frequencies of *N. irene* locally. The results indicate hybridization to be prevented by a “lock-and-key” mechanism, but ♂ *N. irene* often attempt mating with ♀ *N. gracilis*. Contrary to prediction, andromorph frequency in *N. irene* did not depend on whether *N. irene* populations were in sympatry or allopatry with *N. gracilis*. As predicted, *N. irene* ♂♂ attempted tandem formation most frequently with conspecific gynomorphs, while

N. gracilis ♂♂ made most heterospecific tandem attempts on *N. irene* andromorphs. Collectively, these results suggest that *N. gracilis* ♀♀ may be frequently harassed by *N. irene* ♂♂, and that this may help explain the relative rarity of *N. gracilis*.

- (18866) VERBERK, W.C.E.P., J.T. KUPER, L.P.M. LAMERS, M.J.A. CHRISTIANEN & H. ESSELINK, 2007. Restoring fen water bodies by removing accumulated organic sludge: what are the effects for aquatic macroinvertebrates? *Proc. Neth. ent. Soc. Meet.* 18: 115-124. – (First Author: Dept Anim. Ecol. & Ecophysiol., Radboud Univ., Nijmegen, The Netherlands).

Erythromma najas and *Pyrrhosoma nymphula* were found in small numbers after dredging in Molenpolder and/or Sluipwijk, The Netherlands.

- (18867) YASUOKA, J. & R. LEVINS, 2007. Ecology and vector mosquitoes in Sri Lanka: suggestions for future mosquito control in rice ecosystems. *SEast Asian J. trop. Med. publ. Health* 30(4): 646-657. – (Dept Pop. & Int. Health, Harvard Sch. Public Health, Bldg 1, Rm 1219, 665 Huntington Ave, Boston, MA 02115, USA).

Out of 5 *Anopheles* and *Culex* spp. considered, the association of odon. larvae with *A. annularis* larvae was significantly correlated in the seepage pool habitats in the Habaraluwewa area, situated within a high malaria risk region in S Sri Lanka.

- (18868) ZHOU, Z., 2007. *Taxonomic and faunistic studies on the superfamily Calopterygoidea from China (Odonata: Zygoptera)*. Diss Inst. Ent., Guizhou Univ., Guiyang. vii + 79 pp. ISBN none. (Chin., with Engl. s. & Engl. descriptions of the new taxa). – (Author's current address unknown).

The morphology, taxonomy and faunal analysis of the Chinese Calopterygoidea (4 fam., 20 gen., 84 spp.) are presented. *Mnais leigongshanus* sp. n. (holotype ♂: Leigongshan, Guizhou prov., 31-V-2005), *Bayadera unimaculata* sp. n. (holotype ♂: Leigongshan, Guizhou prov., 3-VI-2005) and the ♀ allotype of *Rhinocypha maolanensis* Zhou & Bao, 2002 are described and illustrated. The faunal structures at generic and specific levels were examined. 20 known gen. only constitute 3 types of distribution in zoogeographic regions in the world. Among them, 12 gen. are distributed in the oriental region, which make up 60%, while 7 gen. in oriental + Palaearctic region, accounting for 35%. 20 gen. in total are distributed in

the oriental region, accounting for 100%. It is clear that the oriental gen. make up the majority of the Chinese Calopterygoidea at generic level. 84 known spp. are mainly distributed in the oriental region, in which the number of spp. makes up 83.33% of Chinese spp. in total. All the known spp. constitute 16 types of distribution in 7 Chinese zoogeographic sub-regions. Among them, 16 spp. are present only in central China sub-regions, 15 in S China sub-regions, 10 in central China + S China sub-regions, 9 in SW China sub-regions, 9 in SW China + S China sub-regions, 8 in central China + S China sub-regions, accounting for 19.05%, 17.86%, 11.90%, 10.71%, 10.71% and 9.52%, respectively. It is obvious that oriental spp. make up the majority of Chinese Calopterygoidea at species level and they occur mainly in central China and S China sub-regions.

2008

- (18869) BENARD, M.F. & S.J. McCAULEY, 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. *Am. Nat.* 171(5): 553-567. – (First Author: Dept Ecol. & Evol. Biol., Univ. Michigan, Ann Arbor, MI-48109, USA).

Intraspecific comparison of body size and dispersal rate in odon. have found a positive relationship between size and dispersal (cf. *OA* 7377, 8371, 13519). For example: when *Enallagma boreale* larval environment was experimentally manipulated and then the consequences of environmental environment on both body size at metamorphosis and dispersal probability evaluated, individuals that dispersed were significantly heavier at emergence than those that did not disperse. Thus, there is a linkage between environmental conditions, adult phenotype and dispersal behaviour. High-quality habitats produced larger individuals with greater dispersal abilities, which is a potentially common form of the habitat condition-dispersal ability relationship. This suggests that high-quality habitats may contribute a greater proportion of dispersers to the regional pool. Although the "habitat conditions" were experimental treatments, the differences between these treatments parallel those observed in natural environments, demonstrating that habitat conditions produce asymmetric dispersal patterns between natural habitats that differ in larval resource availability.

- (18870) BOGDANOVIĆ, T., E. MERDIĆ & J. MIKUSKA, 2008. Data to the dragonfly fauna of lower

- Neretva river. *Ent. Croat.* 12(2): 51-65. (With Croat. s.). – (Dept Biol., Univ. Osijek, Trg Ljudevita Gaja 5, HR-31000 Osijek).
The research history of odon. exploration on the Neretva delta (Croatia) covers over 140 yr, but the present paper presents the results of the first systematic survey ever conducted there and includes also all the previously published records. Currently, 48 spp. are known to occur in the delta (i.e. 24.44% of the fauna of the Mediterranean). The locality data and dates are listed and the fauna is briefly discussed).
- (18871) BOUIDIN, C. & Y. ROCHEPAULT, 2008. Habitat des larves de la libellule *Somatochlora brevicincta* Robert en Minganie, Québec, Canada. *Naturaliste can.* 132(2): 30-37. – (Authors' addresses not provided).
The *S. brevicincta* habitat in a marsh at Minganie, Quebec (Canada) is described in detail. It is a shallow, mineral-rich depression at the edge of rain-fed fens. The bottom is covered by *Sphagnum* and *Cladodiella* fluitans and there are emergent *Rhynchospora* and *Carex*, and *Drosera* and *Scheuchzeria palustris* also occur.
- (18872) CALLE, P., B. BEEKERS, H. WIJNHOFEN & J. SCHAFFERS, 2008. *De fauna van de Gelderse Poort*. – [*The fauna of the Gelderse Poort*]. Stichting Flora & Fauna Gelderse Poort. 46 pp. (Dutch). – (Address not stated).
Includes a list of 45 odon. spp. recorded during 2003-2007, with detailed annotations on 19 spp.; – Gelderland prov., The Netherlands.
- (18873) COLLIER, K.J. & A. LILL, 2008. Spatial patterns in the composition of shallow-water macroinvertebrate communities of a large New Zealand river. *N.Z. J. Mar. Freshw. Res.* 42: 129-141. – (Environment Waikato, P.O. Box 4010, Hamilton, NZ). *Austrolestes colenisonis* and *Xanthocnemis zealandica* are recorded from the lower Waikato river.
- (18874) DJIKANOVIĆ, V., D. JAKOVCEV-TODOROVIĆ, V. NIKOLIĆ, M. PAUNOVIĆ & P. CAKIĆ, 2008. Qualitative composition of communities of aquatic macroinvertebrates along the course of the Golijska Morava river (West-central Serbia). *Arch. biol. Sci.*, Belgrade 60(1): 133-144. (With Serb. s.). – (First Author: S. Stanković Inst. Biol. Res., RS-11060 Belgrade).
- Gomphus vulgatissimus* is reported from the Pakašnica stream (alt. 646 m) and Senjak on the Moravica (alt. 442 m).
- (18875) GÜNTHER, A., 2008. *Vergleichende Untersuchungen zum Reproduktionsverhalten Südostasiatischer Chlorocyphidae und Calopterygidae*. Diss. Dr rerum naturalium, Techn. Univ. & Bergakad. Freiberg, Freiberg. xix+208 pp. (With Engl. s.). – (Author: Arbeitsgr. Biologie/Ökologie, Inst. Bio-wiss., TU Bergakademie Freiberg, Leipziger Str. 29, D-09599 Freiberg).
A comparative study is presented on the reproductive behaviour of SE Asian members of the 2 families. Many spp. exhibit highly complex and specialized reproductive behaviour, involving territoriality based on limitation of resources. ♂♂ display specialized, species-specific agonistic behaviour, and in most spp. mating is preceded by ritualized courtship of ♀♀ by ♂♂. In both cases visual communication involving ritualised display of ornamentation is of great importance. Inter- and intra-sexual signals are potentially part of mate recognition systems, which have evolved within communities of syntopic spp. This thesis examines the possibilities of using knowledge of reproductive behaviour to differentiate taxa and to help reconstruct their phylogenetic relationships. The study was based on the analysis of behaviour in different parts of SE Asia and New Guinea, involving direct observation, partially supported by video footage. Sufficiently replicated and representative behavioural data for quantitative analysis was available for 17 chlorocyphid taxa (*Aristocypha*, *Disparocypha*, *Heliocypha*, *Libellago*, *Rhinocypha*) and for the calopterygid *Neurobasis kaupii*. For 14 of the 18 taxa no behavioural data had been hitherto published except by the present author. For a further 13 chlorocyphids and 4 *Neurobasis* spp. supplementary data was available. This account provides information on courtship behaviour and on territorial and oviposition behaviour, circadian activity and habitat requirements.
- (18876) KAWNSAR-UL, Y., A.K. PANDIT & S.A. WANI, 2008. Some aspects of habitat ecology of aquatic entomofauna in two freshwater lakes in Kashmir Himalaya. *Proc. 12th World Lake Conf.*, pp. 1916-1921. – (Second Author: Aquat. Ecol. Lab., P.G. Dept Envir. Sci., Univ Kashmir, Srinagar-190006, J&K., India).
The fauna of the Dal (alt. 1586 m) and Nilnag (alt.

- 2180 m) in the Srinagar distr., (India) was examined. 5 odon. gen. are listed.
- (18877) LEMELIN, R.H., 2008. Dragonfly tourism. *In*: M. Luck, [Ed.], *Encyclopedia of tourism and recreation in marine environments*, p. 145, Cobi Wallingford, 9781845933500. – (Author: Sch. Outdoor Recreation, Parks & Tourism, Lakehead Univ., Thunder Bay, ON, P7B 5E1, CA).
[Main part, almost verbatim and without bibl. references] – While the activity of enjoying Odon. is a relatively new leisure phenomenon in Western society, in some Asian countries, such as China and Japan, dragonflies have a long history of being involved in popular culture and are even raised as pets. Dragonfly gatherings (e.g. counts, educational outings, meetings etc.) as well as dragonfly watching and photographing are in Europe and N America increasing in popularity. Dragonflies are also viewed in various sanctuaries found in Europe and Japan. The most notable attraction may perhaps be the dragonfly awareness trails located in the National Botanical Gardens in Pietermaritzburg, Sth Africa. Conservative estimates place the number of Odon. enthusiasts belonging to a formal association at over 3000 worldwide. this number increases dramatically if one was to include participants in the growing number of dragonfly events. Facilitating the growth of these leisure activities, but more specifically the dragonfly watching, is the availability of ever increasing number of national, regional and local field guides and dragonfly websites.
- (18878) McCAULEY, S.J., 2008. Slow, fast and between habitat distribution and behaviour of larvae in nine species of libellulid dragonfly. *Freshw. Biol.* 53: 253-263. – (Dept Ent., Cent. Pop. Biol., Univ. California, 2320 Storer Hall, One Shields Ave, Davis, CA-95616, USA).
Activity and microhabitat use are important factors determining species performance in habitats that differ in permanence and species composition of top predators. This study examined the relationship between the distribution across a gradient of habitat permanence and an associated transition in the composition of top predators and the behaviour of larvae of 9 Anisoptera spp. It also assessed the relationship between larval behaviour, body size and the duration of the larval stage. In laboratory mesocosms the mobility of the different spp. was measured, as was the extent to which they associated with artificial vegetation. Species mobility was positively related to their natural occurrence in habitats in which invertebrates or small-bodied fish were the top predators, and negatively related with the frequency with which species co-existed with large-bodied fish, the permanence of the habitat and the length of the larval stage. Rather than falling into strict low and high mobility categories, habitat generalists that occurred across the habitat gradient, co-existing with different top predators, had variable mobility levels. In these generalists, mobility was positively related to how frequently they were found in natural habitats in which invertebrates were the top predators. The extent to which spp. utilized the artificial vegetation in mesocosms was associated with the length of the larval period but was not associated with mobility or a sp. habitat distribution in the field.
- (18879) McCAULEY, S.J., C.J. DAVIS & E.E. WERNER, 2008. Predator induction of spine length in larval *Leucorrhinia intacta* (Odonata). *Evol. Ecol. Res.* 10: 435-447. – (First Author: Dept Ent., Cent. Pop. Biol., Univ. California, 2320 Storer Hall, One Shields Ave, Davis, CA-95616, USA).
Larvae collected from ponds with fish present had longer spines than larvae collected from ponds without fish. In the experiment, exposure to fish resulted in longer spines from some but not all of the spines measured. These results indicate that at least some of the variation in spine length is the result of plasticity. *L. intacta* is not a sister species to a European *Leucorrhinia* in which similar plasticity has been found. Mapping plasticity on to the phylogeny of this genus indicates that either plasticity is ancestral to the 2 major clades of this genus or that it has arisen independently twice.
- (18880) MIHOKOVIĆ, N., 2008. Review and checklist of Odonata from Košćec collection in the Municipal Museum Varaždin. Franjo Košćec i njegovo djelo 1882-1968, pp. 255-265, *Croat. Acad. Sci. & Arts* [etc.], Zagreb-Varaždin. (Croat., with Engl. s.). – (Author's postal address not stated).
A commented list of records, referable to 44 spp. from the Varaždin area, Croatia.
- (18881) VAN GOSSUM, H. & T.A. SHERRATT, 2008. A dynamical model of sexual harassment in damselflies and its implications for female-limited polymorphism. *Ecol. Modelling* 210: 212-220. – (First Author: Evol. Biol. Gr., Univ. Antwerp, Groe-

nenborgerlaan 171, B-2020 Antwerp).

♀-limited polymorphism is a widespread phenomenon in Zygoptera. Typically, one ♀ morph resembles the ♂ (the andromorph), while the alternative morph(s) does not (the gynomorph/s). Contemporary explanations for the phenomenon vary, but they generally assume that the polymorphism has arisen as a consequence of frequency-dependent selection on ♀♀ to avoid excessive ♂ harassment. Here, 2 hypotheses are quantitatively characterised: the learned-mate recognition hypothesis (LMR) and the ♂ mimicry (MM) hypothesis. The LMR proposes that ♂♂ learn more quickly to attack the more commonly encountered ♀ morph in the population, so that rarer ♀ phenotypes are harassed relatively less. By contrast, the MM proposes that when andromorphs are initially rare compared to ♂♂, then they are harassed less than gynomorphs, due to their morphological similarity to ♂♂. A parameterised dynamical model of the mating system as a way of quantifying the rate of male harassment of ♀♀ is presented. Subsequently, this information is used in a multi-generational model that includes selection via the differential harassment of morphs and genetic drift, as well as between-year variability in damselfly density and sex ratio. The proportions of andromorphs at selective equilibria were analytically identified. While both the LMR and the MM versions of the model predict no consistent change in the equilibrium proportion of andromorphic ♀♀ with increasing damselfly density, only the MM predicts that the equilibrium proportion of andromorphs should increase with sex ratio. Under low harassment rates (e.g. low population densities and/or low ♂ search rates) selection is absent and ♀ morph frequencies are free to drift. The potential applications of this form of dynamical model for other systems involving sexual harassment are discussed.

- (18882) VON BLANCKENHAGEN, B., 2008. *Nachuntersuchung 2007 zur Verbreitung der Grossen Moosjungfer (Leucorrhinia pectoralis) (Art der Anhänge II und IV der FFH-Richtlinie) in Nord- und Mittelhessen sowie Erarbeitung eines Artenhilfskonzeptes*. Avena, Marburg. iv+31 pp. — (Avena, Nelkenweg 8, D-35043 Marburg).
Includes an overview of *L. pectoralis* occurrence in the federal state of Hessen (Germany) and management suggestions for conservation of its habitats and protection of the sp.

2009

- (18883) AZPILICUETA AMORIN, M., M. VILA & A. CORDERO RIVERA, 2009. Population genetic structure of two threatened dragonfly species (Odonata: Anisoptera) as revealed by RAPD analysis. *In: J.C. Habel & T. Assmann, [Eds], Relict species: phylogeography and conservation biology*, pp. 295-308, Springer, Berlin-Heidelberg. — (Third Author: Dept Ecol. & Anim. Biol., Univ. Vigo, EUET Forestal, Campus Universitario, ES-36006 Pontevedra).
The riverine odon., *Macromia splendens* and *Oxygastra curtisii* were included in the European Habitats Directive as taxa of special concern. Nevertheless, there is almost no genetic information about them. Here, the genetic diversity and population structuring among several NW Iberian locations where these spp. occur is assessed. The genetic pattern revealed by RAPD markers in 4 locations of *M. splendens* and 5 locations of *O. curtisii* was examined. The former showed strong population structuring, whereas gene flow between different river systems may be the reason for the lower structuring inferred for *O. curtisii*. Based on these results, the need of special management for *M. splendens* in NW Iberia is advocated.
- (18884) CARRIÇO, C., J.M. COSTA, T.C. SANTOS & F.M. DA SILVA, 2009. Avaliação da influência de variáveis ambientais na comunidade de formas imaturas de Odonata (Insecta) em dois tributários do rio Timbui, Reserva Biológica da Santa Lécia, Santa Teresa, ES. *Anais 9 Congr. Ecol. Brasil*, 3 pp. (Port.). — (First Author: Inst. Biol., Univ. Fed. Rural Rio de Janeiro, BR 465, Km 7, BR-23890-000 Seropédica, RJ).
The larvae pertaining to 15 gen. are listed from 2 tributaries of rio Timbui (Espírito Santo state, Brazil), viz. the Divisa and the Heloisa Torres streams. The assemblages are similar, but *Brechmorhoga* and *Perithemis* were recorded from the Heloisa Torres only. Features of the respective habitats of the recorded gen. are specified.
- (18885) CARROLI, T.M., 2009. *Resource pulses and spatial subsidies in Ozark karst springs: effects on community structure and food webs*. PhD thesis, Univ. Kansas. x+152 pp. — (Author's current address unknown).
Argia sedula is reported from 3 springs in a karstic region of the Ozarks, SW Green co, Missouri, USA.

- (18886) CHAREST, P., 2009 Première mention au Québec de la demoiselle *Ischnura hastata* (Say, 1839) (Odonata: Coenagrionidae). *Naturaliste can.* 133(1): 29-30. — (Author's address not provided).
2 ♂, 4 ♀, at the bank of a temporary marsh at Mauricie represent the first record of this sp. in Quebec (Canada).
- (18887) CORDERO-RIVERA, A. & S. SANTO-LAMAZZA-CARBONE, 2009. Darwin and the postcopulatory sexual selection. *Revta digital universitaria UNAM* [ISSN 1067-6079] 10(6): 3-12. (Span., with Engl. s.). — (Depto Ecol. & Biol. Animal, Univ. de Vigo, EUET Forestal, Campus Universitario, ES-36005 Pontevedra).
The concept of sexual selection was proposed by Darwin to explain the evolution of secondary sexual characters, i.e. the characters not directly related to the reproductive function, and that clearly do not help their bearers to increase their survivorship. It occurs by means of ♂♂ competition and ♀ choice. Darwin explicitly excluded genital organs from sexual selection, because sexual differences in these characters were believed to be under natural selection only. Over the second half of the 20th century several conceptual revolutions occurred. First, the fights between ♂♂ were prolonged in the time-scale to include the competition between spermatozoa. Second, ♀ choice was widened to include also behaviours and mechanisms taking place after copulation. The time was ready for the development of the idea of "postcopulatory" sexual selection, which was not anticipated in Darwinian texts, perhaps because at that time (end of 19th century) discussing about these concepts was not socially acceptable. The idea of a permanent conflict between ♂♂ and ♀♀ was also added to the current paradigm studying sexual selection, as well as the effect of this force on genital evolution, which has opened a revolutionary field of study, going further away than Darwin ever imagined. — Among the illustrations in the present paper, there is a photograph of 2 *Calopteryx haemorrhoidalis* ♂♂ disputing a ♀, with a paragraph in the text describing this phenomenon in *Calopterygidae*, and another photograph of a rarely occurring intraspecific copulation in *Zygoptera*, showing a ♂ *Ischnura elegans* × ♀ *Pyrrhosoma nymphula* copula.
- (18888) COSTA, J.M., C. CARRIÇO & T.C. SANTOS, 2009. Resultado da primeira expedição científica realizada na ecorregião Xingu-Tapajós pela equipe do setor de insetos aquáticos do Museu Nacional (UFRJ). *Anais 9 Congr. Ecol. Brasil*, 4 pp. (Port.). — (Depto Ent., Mus. Nac., UFRJ, Quinta da Boa Vista, São Cristóvão, BR-20940-040 Rio de Janeiro, RJ).
A brief overview is included of the occurrence of the larvae of 28 odon. gen. in the Xingu-Tapajós region, Brazil.
- (18889) DE OLIVEIRA, D.E. & P. DE MARCO, Jr, 2009. Is there a trade-off between the melanin allocated to the immune system and to camouflage on larvae of the dragonfly *Micrathyrus catenata* Calvert, 1909 (Odonata: Libellulidae)? *Neotrop. Biol. conserv.* 4(3): 133-136. (With Port. s.). — (Second Author: Lab. Ecol. Teórica & Síntese, Depto Ecol., Univ. Fed. Goiás, C.P. 131, BR-74001-970 Goiás).
There is no trade-off. This may be due to the circumstance that the immune system in *M. catenata* larvae is not limited to the acquisition of resources or the camouflage does not demand melanin enough to influence the immune system.
- (18890) GIRILOVICH, I.S. & M.A. DZHUS, 2009. *Pamyatnik prirody respublikanskogo znacheniya "Dubrava": putevoditel'*. — [*Natural monument of national importance "Dubrava": a guide*]. Belarus Natn. Univ. (BGU), Minsk. 93 pp. (Russ.). — (Publishers: Prospect Nezavisimosti 4, BY-220050 Minsk).
This is a guide for biology students of the Belarus Natn. University. The protected area (surface 24 ha) is situated SW of Minsk (Belarus). 14 odon. spp. are listed (pp. 75-76).
- (18891) HOLUŠA, O., 2009. Notes on the first record of *Somatochlora meridionalis* (Odonata: Corduliidae) in the Czech Republic. *Acta Mus. beskid.* 1: 89-95. (With Czech s.). — (Bruzovská 420, CZ-738-01 Frýdek-Místek).
3 ♂ and 1 ♀ and the oviposition were discovered nr Vlahovice-Vrbětice in SE Czech Republic (13 & 17-VII-2006). The potential expansion of the population is discussed.
- (18892) HOLUŠA, O., 2009. Tajemné lesní vážky: kde můžeme u nás spatřit páskovce? — [The mysterious forest dragonflies: where there occur with us the golden-ringed dragonflies?]. *Vesmír* 88(July/Aug.): 2-4. (Czech). — (Bruzovská 240, CZ-738-01 Frýdek-Místek).

- On the habitats of *Cordulegaster bidentata*, *C. boltonii* and *C. heros* in the Czech Republic.
- (18893) HOLUŠA, O., 2009. The finding of *Soma-tochlora sahlbergi* (Odonata: Corduliidae) in the northern Norway. *Acta Mus. beskid.* 1: 97-102. – (Bruzovská 420, CZ-738-01 Frýdek-Místek). A ♀ from Gandvik village (Sør-Varanger, Finnmark prov.), alt. 81 m (29-VII-2001) is brought on record. The habitat is described and the ecological requirements of the sp. are briefly discussed.
- (18894) HONG, S.-J., 2009. Surface ultrastructure of *Plagiorchis muris* growth and developmental stages in rats, the final host. *Parasitol. Res.* 105: 1077-1083. – (Dept Medical Envir. Biol., Chung-Ang Univ. Coll. Medicine, Tongjak-ku, Seoul-156-756, Korea). Metacercariae of the fluke were obtained from *Sympetrum eroticum*, collected from rice paddies of Yongho-myon (Koseong-gun, Gyeongsangnam-do, Korea).
- (18895) JACOBS, C.A., 2009. Wildlife records at Pentsthorpe. *Norfolk Netterjack / Q. Bull. Norfolk & Norwich Naturalists' Soc.* 106: 6-8. – (c/o Ed., F. Farrow, 'Heathlands', 6 Havelock Rd, Sheringham, Norfolk, NR26 8QD, UK). Records of *Calopteryx splendens* and *Ischnura elegans* (25-V-2009), Norfolk, UK.
- (18896) KALISZEWICZ, A. & J. UCHMAŃSKI, 2009. Damage released prey alarm substances or predator odours? Risk assessment by an aquatic oligochaete. *Hydrobiologia* 618: 57-64. – (Cent. Ecol. Res., Pol. Acad. Sci., PO-05-092 Lomianki). *Ischnura elegans* larvae consumed all *Stylaria lacustris* during a 5 h experiment period. It seems that alarm substances did not achieve the response of the exposed oligochaetes in the experiment. In contrast, the alarm substances released by the crashed conspecific worms and added to the water achieved the required concentration. This suggests that *S. lacustris* responds to alarm cues released by damaged prey rather than by substances released by the predator. In the experiment, *Ischnura* odors were constantly present in the water. The lack of response by *S. lacustris* to chemical presence of zygopteran larvae feeding on it may be explained by a minor role of this predator in oligochaete assemblages. However, no other predator seems to be as effective as the odon. larvae. Previous studies have shown that a significant increase in *S. lacustris* abundance was observed after the addition of insecticide, which eliminated all insects, including predators, such as the zygopteran larvae.
- (18897) KALYONCU, H. & H. GULBOY, 2009. Benthic macroinvertebrates from Dariören and Isparta streams (Isparta/Turkey): biotic indices and multivariate analysis. *J. appl. biol. Sci.* 3(1): 79-86. – (Dept Biol., Fac. Sci. & Arts, Demirel Univ., TR-332260 Isparta). *Epallage fatima* and 4 other odon. gen. are listed from the Isparta stream and its 2 tributaries (SW Turkey).
- (18898) LORENZO-CARBALLA, O.M. & A. CORDERO-RIVERA, 2009. Thelytokous parthenogenesis in the damselfly *Ischnura hastata* (Odonata, Coenagrionidae): genetic mechanisms and lack of bacterial infection. *Heredity* 103: 377-384. – (Depto Ecol. & Biol. Animal, Univ. de Vigo, EUET Forestal, Campus Universitario, ES-36005 Pontevedra). Thelytokous parthenogenesis, the production of ♀-only offspring from unfertilized eggs, has been described in all the insect orders, but is a rare phenomenon in the Odon. The only-known case of parthenogenesis in this group is the North American *I. hastata*, which has parthenogenetic populations in the Azore Islands. Here are presented the results of laboratory rearing, which showed parthenogenetic reproduction in the Azorean *I. hastata* populations. In an attempt to understand how parthenogenesis could have evolved in this sp., the genetic mode of parthenogenesis was determined by analysing the genotype of parthenogenetic ♀♀ and their offspring at 3 polymorphic microsatellite loci. In addition, polymerase chain reaction amplification was used to test whether parthenogenesis in *I. hastata* could be bacterially induced. The results indicate that thelytoky is achieved through an (at least functionally) apomictic mechanism and that parthenogenesis is not caused by endosymbionts. Possible routes to parthenogenetic reproduction, as well as the evolutionary implications of this type of parthenogenesis are discussed.
- (18899) NINOMIYA, T. & K. YOSHIZAWA, 2009. A revised interpretation of the wing base structure in Odonata. *Syst. Ent.* 34: 334-345. – (Second Author: Syst. Ent., Grad. Sch. Agric., Hokkaido Univ., Sapporo, 060-8589, JA). Homology of the wing base structure in the Odon. is highly controversial, and many different interpreta-

- tions of homology have been proposed. In extreme cases, 2 independent origins of insect wings have been suggested, based on comparative morphology between the odon. and other pterygote wing bases. Difficulties in establishing homology of the wing base structures between Odon. and other Pterygota result mainly from their extreme differences in morphology and function. In the present paper, homology is established of the wing base structures between Neoptera, Ephemeroptera and Odon. using highly conservative and unambiguously identifiable characters (the basal wing hinge and subcostal veins) as principal landmarks. Homology of the odon. wing base structure with those of Ephemeroptera and Neoptera can be identified reliably. Based on this interpretation, the ancestral condition of the insect wing base structure is discussed.
- (18900) PRUNIER, F., 2009. Nueva cita de *Oxygastera curtisii* (Dele, 1834) (Odonata: Corduliidae) en la provincial de Sevilla. *Boln Soc. andaluza Ent.* 16: 45-47. – (Author's postal address not stated). 1 larva, Rivera del Ciudadeja, Siera Morrena (Spain), 16-III-2008. The habitat is described in detail.
- (18901) PRUNIER, F., 2009. Presence of *Macromia splendens* (Pictet, 1843) (Odonata: Corduliidae) in the Tranco de Beas reservoir (Jaén). *Zool. baetica* 20: 97-99. (Span., with Engl. title). – (Author's postal address not stated). 1 larva, Parque Natural de las Sierras de Cazorla (alt. 620 m), 30-VIII-2007; – Spain.
- (18902) RACZYŃSKA, M. & J.C. CHOJNACKI, 2009. The structure of macrozoobenthic communities in the Tywa river, a right-bank tributary of the Oder river (Northwest Poland). *Oceanol. Hydrobiol. Stud.* 38(3): 31-42. – (Dept Marine Ecol. & Envir. Prot., W Pomeranian Univ Technol., Królewiczka 4/H, PO-71-550 Szczecin). The odon. density at the individual sampling sites is stated (orderwise) in a tab., but no reference is made to dragonflies in the text.
- (18903) REELS, G.T., 2009. Dragonfly emergence at a small newly-created pond in Hong Kong. *Hong Kong ent. Bull.* 1(2): 32-37. – (H-3-30 Fairview Park, Yuen Long, N.T., Hong Kong, China). The pond was created in 2003, the observations on Anisoptera emergence were carried out from March 2004 to July 2005. The exuviae were much more abundant in 2004 than in 2005, which is probably due to the growth and proliferation of the predatory fish in the pond. Most aeshnids and libellulids emerged in March and Apr. 2004. *Anax guttatus* had a second pulse of emergence in June 2004. The exuviae of *Sinictinogomphus clavatus*, *Ictinogomphus pertinax* and *Epophthalmia elegans* first appeared in June or July 2004, but the 2 gomphids emerged in greater numbers in Apr. and May 2005.
- (18904) REIMER, R.W., G.R. FEULNER & J.R. HORNBY, 2009. Errata and addenda: Updated illustrated checklist of dragonflies of the UAE, including a third species of *Ischnura* damselfly. *Tribulus* 18: 28-36. – (First Author: UAE Univ., UGRU-ITS, P.O. Box 17172, Al Ain, UAE). *I. fontaineae* is added to the checklist as listed in *OA* 18856, bringing the status of the known United Arab Emirates spp. up to 27. Some errors in the identification of the photographs in that paper are corrected, but the corrections do not alter the number of the known spp.
- (18905) SALWINIA EKOKLUB, [Eds], 2009. [*Biodiversity of the Tuga river: a guide*]. Salwinia Ekoklub, Nowy Dwór Gdański. iv + 39 pp. ISBN 978-83-911771-2-9. (Pol.). – (Address not stated). 6 odon. spp. are listed from the river (Poland). The Author of the list is Dr M. Grabowski; the correctness of *Coenagrion armatum* identification may be questionable.
- (18906) SHARMA, G., V.V. RAMAMURTHY & R. KUMAR, 2009. Collection of damselflies and dragonflies (Odonata: Insecta) in National Pusa Collection, Division of Entomology, Indian Agricultural Research Institute, New Delhi, India. *Biol. Forum* 1(2): 47-50. – (Second Author: Natn. Pusa Coll., Div. Ent., Indian Agric. Res. Inst., Pusa Campus, New Delhi, India). A checklist of 273 spp., without locality data.
- (18907) TATARINOV, A.G. & O.I. KULAKOVA, 2009. *Fauna evropeyskogo severo-vostoka Rossii*, Vol. 10. *Strekozy*. – [*Fauna of the European northeastern Russia*, Vol. 10. *Dragonflies*]. Nauka, Sankt-Peterburg. 214 pp. ISBN 5-02-025945-4. – (Russ.). The larvae and adults of 50 spp. are described and keyed, and a biogeographic analysis of the fauna is presented.

- (18908) VAN OOSTERHOUT, M.P., G. VAN DER VELDE & J.G. GEIGHER, 2009. High altitude mountain streams as a possible refuge habitat for the catfish *Amphilius uranoscopus*. *Envir. Biol. Fish* 84: 109-120. – (First Author: Dept Anim. Ecol. & Ecophysiol., Inst. Water & Wetland Res., Radboud Univ., Heyendaalseweg 135, NL-6525 AJ Nijmegen). 6 odon. fam. are listed among the macroinvertebrate fam. recorded in samples from the Limpopo river (alt. 1300-1400 m; Sth Africa). Based on stable isotope analysis, the platynemidid, gomphid, corduliid and libellulid spp. were consumed by the catfish.

2010

- (18909) ALBERTI LUBERTAZZI, M.A. & H.S. GINSBERG, 2010. Emerging dragonfly diversity at small Rhode Island (USA) wetland along an urbanization gradient. *Urban Ecosyst.* 2010: 17 pp.; – DOI: 10.1007/s 11252-010-0133-8; – (First Author: Dept Plant Sci. & Ent. Woodward Hall, Univ. Rhode Island, Kingston, RI 02881, USA).
Natal habitat use by Anisoptera was assessed on an urban to rural land-use gradient at a set of 21 wetlands, during 2 emergence seasons. The wetlands were characterised for urbanisation level by using the first factor from a principal components analysis combining chloride concentration in the wetland and percent forest in the surrounding buffer zone. Measurements of species diversity and its components (species richness and evenness) were analysed and compared along the urbanization gradient, as were distributions of individual spp. Dragonfly diversity, species richness, and evenness did not change along the urbanisation gradient, so urban wetlands served as natal habitat for numerous spp. However, several spp. displayed strong relationships to the degree of urbanisation, and most were more commonly found at urban sites and at sites with fish. In contrast, relatively rare spp. were generally found at the rural end of the gradient. These results suggest that urban wetlands can play important roles as dragonfly habitat and in dragonfly conservation efforts, but that conservation of rural wetlands is also important for some spp.
- (18910) ALTAMIRANDA-S., M., L.A. PEREZ-G. & L.C. GUTIERREZ-M., 2010. Composición y preferencia de microhábitat de larvas de Odonata (Insecta) en la siénaga San Juan de Tocagua (Atlántico, Colombia). *Caldasia* 32(2): 399-410. (With

Engl. s.). – (First Author: Mus. Ent. Francisco Luis Gallego, Univ. Nac. Colombia, Apdo 3840, Medellín, Colombia).

The response of odon. larvae (14 spp.) to the available substrates on the shoreline of the San Juan de Tocagua swamp (Atlántico, Colombia) is assessed.

- (18911) BEATTY, C.D., S. FRASER, F. PEREZ-JVOSTOV & T.N. SHERRATT, 2010. Dragonfly and damselfly (Insecta, Odonata) distribution in Ontario, Canada: investigating the influence of climate change. *BioRisk* 5: 225-241. – (First Author: Dept Biol., Santa Clara Univ., 500 E1 Camino Real, Santa Clara, CA 95053, USA).

Temperature data and odon. distribution data collected over approx. 60 yr were analysed. Analysis of temperature data from 31 weather stations collected in the years 1945-2000 showed an overall significant increase in the minimum, maximum and mean monthly temperatures; these trends were not adjusted for changes in urbanisation. Comparison of county level presence/absence data for odon. from the 1950's and 2002 found a slight decrease in the northernmost distributions of some spp., although no significant patterns were evident. Lower sampling coverage in the larger, more northerly counties in Ontario, as well as the assessment of distributions based on county records may limit the sensitivity of this approach in detecting changes in odon. species distributions over time. Future work should focus on increasing the coverage, uniformity and geographic detail of available datasets, as well as evaluating range change through testing predictions based on the ecology and biogeography of spp.

- (18912) BECHLY, G., 2010. Fossile Insekten aus den Plattenkalken der Crato-Formation. *Messekatalog Mineralien Tage München* 2010: 105-111. – (Staat. Mus. Naturk., Rosenstein 1, D-70191 Stuttgart).
General, includes a photo of *Cratostenophlebia schwickerti*.

- (18913) BUDEN, D.W., 2010. *Pantala flavescens* (Insecta: Odonata) rides West winds into Ngulu atoll, Micronesia: evidence of seasonality and wind-assisted dispersal. *Pacif. Sci.* 64(1): 141-143. – (Dept Nat. Sci. & Mathem., Coll. Micronesia, P.O. Box 159, Colonia, Pohnpei-96941, F.S. Micronesia).
Observations on *P. flavescens* represent the first odon. record for the atoll (Micronesia), but descriptions by local residents of a large, rarely encountered, blue

- dragonfly may pertain to *Anax guttatus*. The sudden appearance of *P. flavescens* on Ngulu, after its apparent absence during 2 and a half weeks of the study, together with the absence of exuviae in potential breeding sites and remarks by local residents alluding to its appearance each yr around Aug. and Sept., suggests that it occurs regularly in migration and that there is no permanent resident population. Its appearance often coincides with winds from westerly direction.
- (18914) DA SILVA, A.L.L., 2010. *Diversidade e variação espaço-temporal da comunidade de macroinvertebrados bentônicos em uma laguna costeira subtropical no sul do Brasil*. Diss. Mestre em Ecologia, Univ. Fed. Santa Catarina, Florianópolis/SC. 87 pp. (Port.). – (Ecologia, Cent. Ciênc. Biol., Univ. Fed. Santa Catarina, Campus Universitario s/n, Trindade, BR-88040-970 Florianópolis, SC). Includes information on seasonal and spatial abundance of the larvae of 8 odon. gen. in the coastal lake of Peri, situated in the S of Santa Catarina state (S Brazil).
- (18915) DUPONT, P., 2010. Plan national d'actions en faveur des odonates. OPIE, Ghuyancourt. x + 159 pp. – (Office pour les insectes et leur environnement, OPIE, B.P. 30, F-78041 Guyancourt cédex). This is the French National Action Plan for 18 threatened spp., of which some are also endangered on the European level. Its objectives are to: (1) assess and improve the conservation status of these spp. in France through the improvement of the knowledge on ecology, distribution and the required conservation management; – (2) design a conservation management at different landscape scales in order to increase the habitat quality; and – (3) provide the communication and training of the concerned actors.
- (18916) EWALD, N. et al. [17 joint authors], 2010. *A preliminary assessment of Important Areas for Ponds (IAPs) in the Mediterranean basin and Alpine arc*. Techn. Rep. Europ. Pond Conserv. Network, EPCN, Jussy/Geneva. iii + 41 pp. – (Publishers: EPCN, c/o Hepia, Univ. Appl. Sci. Western Switzerland, CH-1254 Jussy/Geneva). It covers Spain, Portugal, France, Italy, Malta, Greece, Albania, Montenegro, Morocco, Algeria, Tunisia and Middle East. 21 odon. spp. associated with ponds in this area are listed.
- (18917) FERLAND-RAYMOND, B., R.E. MARCH, C.D. METCALFE & D.L. MURRAY, 2010. Prey detection of aquatic predators: assessing the identity of chemical cues eliciting prey behavioural plasticity. *Biochem. Syst. Ecol.* 38: 169-177. – (First Author: Dept Biol., Trent Univ., 1600 W Bank Dr., Peterborough, ON, K9J 7B8, CA). Chemical cues transmitted through the environment are thought to underline many prey responses to predation risk, but despite the known ecological and evolutionary significance of such cues, their basic composition is poorly understood. Using *Rana septentrionalis* and *R. catesbeiana* tadpoles (prey) and *Anax junius* and libellulid larvae (predators), chemical cues associated with predation risk are here identified via solid phase extraction and mass spectrography of the extracts. It was found that odon. larvae predators consistently produced a negative ion, m/z 501.3, when they fed on the tadpoles, but this ion was absent when dragonflies were fasted or fed invertebrate prey. When tadpole behavioural responses to dragonfly chemical cues were examined, tadpoles reduced their activity, particularly in response to dragonflies feeding on tadpoles. Furthermore, a negative correlation was noted between the level of tadpole activity and the concentration of the m/z 501.3 compound in odon. feeding trials, indicating that this ion was possibly responsible for tadpole anti-predator behaviour.
- (18918) GOFFART, P., 2010. Southern dragonflies expanding in Wallonia (South Belgium): a consequence of global warming? *BioRisk* 5: 109-116. – (Observatoire de la Faune, Flore, Habitats, Direction de la Nature et de l'Eau, Ave. Marécha Juin 23, B-5030 Gembloux). The occurrence and abundance of *Coenagrion scitulum*, *Lestes barbarus*, *Aeshna affinis*, *Anax parthenope*, *Crocothemis erythraea*, *S. fonscolombii* and *S. meridionale* in Wallonia was analysed for the period 1981-2000. The rise of temperature appears to be the main factor explaining their continuous expansion.
- (18919) GOŁAB, M.J., M. POTOCZEK & S. ŚNIEGULA, 2010. New records of *Cordulegaster bidentata* Selys, 1843 (Odonata: Cordulegasteridae) from the Beskid Wyspowy Mts and the Bieszczady Mts. *Wiad ent.* 29(3): 1 p. (Pol., with Engl. title). – (Inst. Ochrony Przyrody, PAN, Kraków, Poland). 6 records (2008, 2009), from 3 localities; – Poland.

- (18920) HACET, N., 2010. Notes on flight periods and distributions of some dragonflies in Turkey. *Munis Ent. Zool.* 5(1): 166-170. – (Dept Biol., Fac. Sci., Trakya Univ., TR-22030 Edirne).
New data on flight periods are given for 11 spp. In Antalya prov., *Anax ephippiger* was recorded as early as in February, though most records are dated from Aug. to Oct. For 6 spp. new locality data are presented.
- (18921) HACET, N., B. CAMUR-ELIPEK & T. KIRGIZ, 2010. A study on the odonate larvae of Turkish Thrace, with larval identification keys to the considered taxa. *J. ent. Res. Soc.* 12(2): 57-74. – (Dept Biol., Fac. Sci., Trakya Univ., TR-22030 Edirne).
Well-illustrated keys are provided for 26 spp. and for most of them some new Thracian distributional records are presented.
- (18922) HOLUŠA, O., 2010. The results of the faunistic research of dragonflies (Insecta: Odonata) in the region of Mistek town. *Acta Mus. beskid.* 2: 63-74. (Czech, with Engl. s.). – (Bruzovská 240, CZ 738-01 Frydek-Mistek).
A commented list of 38 spp. from 25 localities; – N. Moravia, Czech Republic.
- (18923) HOLUŠA, O. & M. KÚDELA, 2010. New records of *Cordulegaster heros* (Odonata: Cordulegasteridae) from its northern range border in Slovakia. *Acta Mus. beskid.* 2: 75-87. (With Czech s.). – (Second Author: Dept Zool., Fac. Nat. Sci., Comenius Univ., Mlynská dolina, SK-842-15 Bratislava-4).
The occurrence of the sp. in 4 regions of western and central Slovakia is outlined, mapped and discussed. It is known from 44 localities, at the elevations between 194 and 516 m.
- (18924) *IDF-REPORT*. Newsletter of the International Dragonfly Fund (ISSN 1435-3393), Vol. 30 (2010). – (c/o M. Schorr, Schulstr. 7/B, D-54314 Zerf).
Marinov, M. & P. McHugh: Comparative study of the Chatham Islands Odonata: morphological variability, behaviour and demography of the endemic *Xanthocnemis tuanuii* Rowe, 1987 (pp. 1-44).
- (18925) JOURDE, P., 2010. Les odonates: biologie et écologie, pts 1 & 2. *Insectes* 157: 3-8; 158: 31-35. – (LPO, La Corderi Royale, B.P. 90263, F-17305 Rochefort Cedex).
General, on European spp.
- (18926) KAIZE, J. & V.J. KALKMAN, 2010. On a collection of dragonflies (Odonata) from the island of Mioswaar (Papua Barat, Indonesia). *Suara Serangga Papua* 5(2): 71-76. (With Bahasa Indonesian s.). – (Second Author: Naturalis, P.O. Box 9517, NL-2300 RA Leiden).
Records of 28 spp. (18-27 Aug. 2009), with notes on selected spp.
- (18927) KISHIDA, O., G.C. TRUSSELL, A. MUGI & K. NISHIMURA, 2010. Evolutionary ecology of inducible morphological plasticity in predator-prey interaction: toward the practical links with population ecology. *Popul. Ecol.* 52: 37-64. – (First Author: Cent. Ecol. Res., Kyoto Univ., Otsu, Shiga, 520-2113, JA).
A review is presented of recent studies on inducible morphological plasticity in predators and their prey with an emphasis on internal and external constraints and how the nature of predator-prey interactions influences the expression of inducible phenotypes. In particular, it is focused on multiple-trait plasticity, flexibility and modification of inducible plasticity, and reciprocal plasticity between predator and prey. Based on the arguments on these issues, future research directions that should better integrate evolutionary and population studies and thus improve our understanding of the role of phenotypic plasticity in predator-prey population and community dynamics are proposed.
- (18928) LANDWER, B.H.P. & R.W. SITES, 2010. The larval Odonata of ponds in the Prairie Region of Missouri. *Trans. Am. ent. Soc.* 136(1/2): 1-105. – (Enns Ent. Mus., Div. Plant Sci., Univ. Missouri, Columbia, MO 65211, USA).
A faunistic inventory of the larval Odon. of ponds in the Prairie Region of Missouri (USA) is presented, along with habitat associations and a taxonomic key to suborders, fam., gen. and known or spp. expected to occur there.
- (18929) LATHA, C. & V.S.G. THANGA, 2010. Macroinvertebrate diversity of Veli and Kadinamkulam lakes, South Kerala, India. *J. envir. Biol.*, Lucknow 31: 543-547. – (Dept Envir. Sci., Univ. Kerala, Kariavattom, Thiruvananthapuram-695581, India).
Lists 3 odon. gen.
- (18930) MARTIN, K.H., 2010. *The transition zone: impact of riverbanks on emergent dragonfly nymphs*,

implications for riverbank restoration and management. PhD thesis, Antioch Univ. New England. iv + 104 pp. – (Author's current address unknown).

The use of riprap in the restoration and stabilization of riverine landscapes is an issue of concern for many ecologists. While current methods of bank stabilization, especially those involving the placement of rocks (riprap) along the waterline, are effective in controlling erosion their presence changes habitat components (slope, substrate composition, near-shore river velocity) at the river-land interface. The additional impacts of river current, water temperature, soil composition, slope, and water level fluctuation, may further imperil emerging larvae. The study was conducted at the Turners Falls Reservoir (Gill, Massachusetts, USA), and its purpose was to document the effects of riprap, location (up-river or downriver of hydroelectric intake/outtake facilities), water level fluctuation, river velocity, air and water temperature, and soil composition on the distance travelled to emergence site by *Gomphus vastus* and *Sonjagaster spiniceps* and the densities of *S. spiniceps*, *G. vastus*, *Neurocordulia yamaskanensis*, *Dromogomphus spinosus*, *Ophiogomphus rup-insulensis*, *Macromia illinoiensis* and *Epicordulia princeps*. Knowledge of conservation status of these spp. is fairly limited, although *S. spiniceps* (threatened), *G. vastus* (species of special concern), and *N. yamaskanensis* (species of special concern) are all currently listed on the Massachusetts Endangered Species list. Species density was determined through exuviae collection, and emergence distance was recorded from the edge of the waterline to the site of attached exuviae. Results of the study indicated that larval response to the observed abiotic features varies both with location and species. The presence of riprap had no significant effect on densities of *S. spiniceps*, *G. vastus*, *N. yamaskanensis*, *D. spinosus*, *O. rupinsulensis*, *M. illinoiensis*, and *E. princeps*, but did significantly reduce the distance travelled from the waterline by both *G. vastus* and *S. spiniceps*. – [Neither in the abstract nor anywhere in the text, the genus names are spelt out]

- (18931) McCAULEY, S.J., 2010. Body size and social dominance influence breeding dispersal in male *Pachydiplax longipennis* (Odonata). *Ecol. Ent.* 2010: 9 pp.; – DOI: 10.1111/j.1365-2311.2010.01191.x – (Dept Ent., Cent. Pop. Biol., Univ. California, 2320 Sorer Hall, One Shields Ave, Davis, CA-95616, USA). Dispersal behaviour can be affected by an individual's

phenotype, by the environmental or social context they experience, and by interactions between these factors. Differential dispersal propensities between individuals may also be an important modifier of functional connectivity between populations. To assess how a key trait, body size, affected both social interactions and dispersal behaviour, this study examined the relationship between body size, antagonistic interactions, and breeding dispersal in δ *P. longipennis* across a seasonal decline in adult body size. During a seasonal peak in δ body size in this study, dispersers were smaller than non-dispersers. Later in the season, the body size of dispersers and non-dispersers did not differ. Focal observations found that body size was related to competitive dominance, large δ δ engaged in aggressive chases more often and smaller δ δ were more frequently pursued. These results indicate that when large δ δ were present, small δ δ were more likely to disperse suggesting that dispersal is a tactic adopted by social subordinates in this context. If breeding dispersal is typically undertaken by subordinate δ δ , functional connectivity between populations may be less than estimated from absolute dispersal rates.

- (18932) MONTROYA MORENO, Y., N. AGUIRRE RAMIREZ, O. CAICEDO & J. PALACIO, 2010. Dinámica multiannual de los macroinvertebrados acuáticos bentónicos en la quebrada Vegas de la Clara. *Invest. Biodiv. Desarrollo* 29(2): 201-210. (Span., with Engl. s.). – (Gr. Invest. GAIA, Fac. Ingeniería, Univ. Antioquia, Medellín, Colombia). 11 odon. gen. were recorded (2005-2009) from Las Vegas stream, Antioquia (Colombia). In a graph, their annual abundance in samples is shown for each yr separately.
- (18933) MÜLLER, G.A., F.T. NAME, F.C.L. PACHECO & C.B. MARCONDES, 2010. Analysis of an alternative method for the study of bromeliad-associated fauna in plants with different foliar organization. *Anais Acad. bras. Ciênc.* 82(4): 903-906. (With Port. s.). – (Last Author: Depto Microbiol. Immunol. & Parasitol., Cent. Ciên. Biol., Univ. Fed. Santa Catarina, Campus Universitário da Trindade, C.P. 476, BR-88040-970 Florianópolis, SC). The traditional method of insect collecting from tank bromeliads requires dismantling of the plant, whereas an alternative is simply sucking of water from the tank and does not seriously damage the plant. The efficiency of the 2 techniques in *Leptagrion* (and some

- other, mostly Diptera) studies is here compared based on collections from *Vriesea friburgensis* (with many water-containing axilles) and *Achmea lindenii* (having a single cavity). The suction from *Vriesea* yields significantly poorer results than those obtained by dismantling of the plant. The suction from *Achmea* is also less effective, but it is still considered here as an adequate method when information on species diversity is required rather than that on population density of Leptagrion in the bromeliads possessing a single water cavity.
- (18934) OMOIGBERALE, M.O. & A.E. OGBEIBU, 2010. Environmental impacts of oil exploration and production on the macrobenthic invertebrate fauna of Osse river, southern Nigeria. *Res. J. envir. Sci.* 4(2): 101-114. – (Dept Anim. & Envir. Biol., Univ. Benin, P.M.B. 1154, Benin, Nigeria).
8 odon. taxa are listed, but most identifications are probably wrong.
- (18935) PESSACQ, P. & J.M. COSTA, 2010. *Epipleoneura angelo* (Odonata: Protoneuridae), a new species from the central region of Brazil. *Zootaxa* 2721: 55-61. (With Port. s.). – (Second Author: Depto Ent., Mus. Nac., UFRJ, Quinta da Boa Vista, São Cristóvão, BR-20.940-040 Rio de Janeiro, RJ).
The new sp. is described, illustrated and compared to *E. williamsoni*. Holotype ♂: Brazil, Mato Grosso, Chapada dos Guimarães, 28-X-1983; – allotype ♀: same data, but Rio Coxipozinho. The types and paratype ♂♂ are deposited in MNUFRJ.
- (18936) REELS, G.T., 2010. Seasonal emergence of dragonflies (Odonata: Anisoptera) at ten ponds in Hong Kong. *Hong Kong ent. Bull.* 2(1): 24-31. – (H-3-30 Fairview Park, Yuen Long, N.T., Hong Kong, China).
The emergence was monitored using emergence traps for periods of varying duration between Feb. 2004 and Sept. 2007. 3 newly created, 5 re-profiled and 2 long-established former commercial fish ponds were included in the study. Exuviae abundance varied considerably between ponds and years, as did the spp. recorded. There was an overall declining trend over the 4-yr period. The causes of these variations were not determined. Anisoptera emergence was strongly seasonal in all 4 yr, with over 80% of total annual emergence occurring during March-May in most ponds. A winter emergence peak, dominated by *Pantala flavescens*, was recorded in ponds which ha only been filled in the preceding summer.
- (18937) ŠÁCHA, D., 2010. Results of the research on dragonflies (Odonata) in the area within the Pieniny National Park. *Pieniny Przyr. Czlowiek* 11: 69-79. (Slovak, with Engl. s.). – (Podtatranského 31, SK-031-01 Liptovský Mikuláš).
Records of 34 spp. Among these, the most noteworthy are *Coenagrion hastulatum*, *Leucorrhinia dubia*, *L. pectoralis*, *L. rubicunda* and *Sympetrum pedemontanum*; – Slovakia.
- (18938) SEFCHICK-EDWARDS, J., 2010. When dragons fly. *Missisquoi Matters / Newsl. Friends Missisquoi Natn. Wildl. Refuge* 2010(summer): 7-8. – (c/o Ed.: 29 Tabor Rd, Swanton, VT 05488, USA).
A kind of a short, almost literary and very personal article on dragonfly habits.
- (18939) SMITH, P.H., 2010. Dragonflies and climate change. *Coastlines* 2010(1): 17. – (c/o Ed.: L. Lander, Sefton Council Planning & Development Dept, Magdalen House, 30 Trinity Rd, Bootie, L20 3NJ, UK).
In Britain, several spp. with mainly southern British distributions have moved North (*Anax imperator*, *Sympetrum sanguineum*). Several migrant spp. (*A. parthenope*, *Sympetrum flaveolum*, *S. fonscolombii*) appear in warm summers. *Calopteryx virgo* has greatly increased in NW England, but this is probably due to the improved water quality rather than to increased temperatures. *Erythromma viridulum* appeared on the Essex coast in 1999 and it now breeds in a large part of SE England. By 2006, it has reached Derbyshire.
- (18940) STOLLARD, J. & J. STOLLARD, 2010. Damsels and dragons. *Wood Duck / Bull. Hamilton Naturalists' Club* 63(8): 175-176. – (HNC, Westdale, P.O. Box 89052, Hamilton, ON, L8S 4R5, CA).
The morphological characterization is presented of the Canadian odon. families, and reference is made to the Hamilton Odonata Count and the Hamilton Odonate Atlas project; – Ontario, Canada.
- (18941) TANG, H.B., L.K. WANG & M. HÄMÄLÄ-INEN, 2010. *A photographic guide to the dragonflies of Singapore*. [With a Foreword by A.G. Orr]. Raffles Mus. Biodiv. Res., Singapore. v + 223 pp. ISBN 978-981-08-61551-1. – (Publishers: Raffles Mus. Biodiv. Res., Univ. Singapore, Science Dr. 2, Singa-

- pore-117546, Singapore).
 [Based on the pdf of the last galley proof] – Currently, 124 spp. are known from Singapore (as to ca 250 spp. recorded from Peninsular Malaysia). This beautifully produced and handy guide facilitates an easy identification of the adults of almost all spp. The introductory chapters provide an outline of dragonfly morphology and biology, with extensive (and most welcome!) considerations on the nature and use of the Engl. common names which, for the same taxa, are often different in different countries. The core of the book are the easily readable, not-technical descriptions of all spp., with brief statements on the respective localities, habitats and habits. The book is richly illustrated with col. photographs, enhancing its attractiveness and facilitating species identification. – (Singapore is also covered by the work described in OA 16217).
- (18942) TARIQCH, M., 2010. *Systematics of dragonflies (Anisoptera: Odonata) of Pakistan*. PhD Thesis, Arid Agric. Univ., Rawalpindi. xiv + 190 pp. – (Dept Ent., Arid Agric. Univ., Rawalpindi, Pakistan). 68 spp. are treated and keyed. *Anaciaeschna jaspidea*, *Anax indicus*, *Gynacanthaeschna sikkima*, *Onychogomphus biforceps*, *Epophthalmia v. vittata*, *Macromia moorei* and *Rhodothemis rufa* are new to the fauna of Pakistan.
- (18943) TOTH, S., 2010. *Dragonfly fauna of the Transdanubian hills and the surroundings*. Natura samogiensis, Vol. 16: 188 pp. ISBN 978-963-7212-72-7. (Hung., with Engl. s.). – (Author: Széchenyi u. 2, HU-8420 Zirc). A comprehensive faunistic monograph (Hungary), presenting 58 spp. from 1070 localities, with precise listing of all specimens (incl. larvae and exuviae), localities and collection dates. UTM-distribution maps and phenology graphs are provided for all spp. The history of odonatol. research in the region is traced from 1896 and an exhaustive bibliography is appended.
- (18944) VENKATESH, A., 2010. Dragonfly: short essay to highlight Odonata as a potential biocontrol agent against vector mosquitoes. *Newsl. Cent. Res. med. Ent.*, Madurai 8(1): 2-3. – (c/o Ed.: Dr B.K. Tyagi, Cent. Res. Med. Ent., ICMR, 4 Sarojini St., Chinna Chikkikulam, Madurai-625005, Tamil Nadu, India). On the role of odon. in mosquito control, with an annotated list of spp. so far either studied in laboratory or used in the field, and with some bibliography related to the subject.
- (18945) WILDERMUTH, H., 2010. Waldlichtungen als terrestrische Habitate von Libellen (Odonata). *Entomo helvetica* 3: 7-24. (With Engl. & Fr. s's). – (Haltbergstr. 43, CH-8630 Rüti). Odon. are generally considered aquatic insects living in or near water. However, during the imaginal period they spend much time in terrestrial habitats often far aside from the breeding sites. In a systematic study at 8 forest clearings with extensively utilized moist meadows E and W of Rüti, canton Zürich (Switzerland), it has been shown that 80% of the local odon. fauna used these terrestrial habitats for maturation, foraging, thermoregulation and exceptionally also as rendezvous. *Platycnemis pennipes* and *Libellula fulva* evidently had to cover distances of 0.7-2.2 km and to fly over forests and cross wide roads in order to reach the clearings and to return to the breeding site. The importance of the clearings for various spp. was different and thus discussed in detail.
- (18946) ZHUKOVA, O.N. & D.M. BEZ-MATERNYH, 2010. [Zoobenthos of the lakes of the North Kazakhstan province]. *Mir Nauki Kultury Obrazovaniya* 6(23): 277-281. (Russ.). – (First Author: IVEP, SO, Russ. Akad. Nauk, Barnaul, Russia). *Coenagrion vernale* (n.n. = *C. lunulatum*) is recorded from 3 lakes.
- (18947) ZIA, A., 2010. *Biosystematics of damselflies (Zygoptera: Odonata) of Pakistan*. PhD Thesis, Arid Agric. Univ., Rawalpindi. 286 p. – (Dept Bio., Fac. Crop & Food Sci., Arid Agric. Univ., Rawalpindi, Pakistan). 51 spp. are treated and keyed. *Libellago l. lineate*, *L. greeni*, *Protosticta hearsayi*, *Coelicia vacca*, “*Cydonolestes*” *cyanea*, *Ellatoneura atkinsoni*, *E. campioni* and *E. souteri* are for the first time recorded from Pakistan. As new is described and illustrated *Indocnemis ahmedi* sp. n. (2 ♂), from Nouser (AJK) and Dasu (NWFP), 11-V-2005 and 1-VI-2006, respectively (pp. 195-202). The holotype is not designated.

2011

- (18948) AYUB BRASIL, M., G. DE FREITAS HORTA, J. FRAXE NETO, T. OLIVEIRA BAPTOS & G. RINALDI COLLI, 2011. Feeding ecology of

- Acanthochelys spixii (Testudines, Chelidae) in the Cerrado of central Brazil. *Chelonian Conserv. Biol.* 10(1): 91-101. – (First Author: Biol. Anim., Univ. Brasilia, BR-70910-900 Brasilia, DF).
- Coenagrionidae, Lestidae, Aeshnidae, Gomphidae and Libellulidae larvae are reported among the food items of the turtle in the Parque Nacional de Brasilia (DF).
- (18949) BAHAAAR, S.W.N. & G.A. BHAT, 2011. Taxocoenosis and distribution of nektonic fauna in the rice fields of Kashmir (J and K), India. *Pakistan J. biol. Sci.* 14(8): 483-489. – (Terrest. Ecol. Lab., Dept Envir. Sci., Univ. Kashmir, Srinagar-190006, J & K, India).
Among the almost 12.000 invertebrate and vertebrate (fish, amphibians) specimens collected from 6 rice fields by lowering a metal frame into the water and lifting it after 15 min (V-VIII, 2005, 2006), there was a single “dragonfly nymph” in a nekton sample from Pulwama (S Kashmir).
- (18950) BARNARD, P.C., 2011. Order Odonata: the dragonflies and damselflies. In: P.C. Barnard, *The Royal Entomological Society book of British insects*, pp. 42-48, Blackwell, London.
A book chapter, presenting an overview of British odon. families and a list of the 3 spp. of special Conservation Concern in the UK, viz.: Coenagrion mercuriale, Aeshna isosceles and Oxygastra curtisii.
- (18951) BEDJANIČ, M., 2011. Preliminarna ocena izvedljivosti načrtovane prostorske ureditve ob Rudniškem jezeru v Kočevju: kačji pastirji (Odonata). – [Preliminary assessment of the feasibility of the proposed urbanization at Rudniško lake in Kočevje: dragonflies (Odonata)]. Bedjanič, Slovenska Bistrica. 23 pp. (Slovene). – (Kolodvorska 21/B, SI-2310 Slovenska Bistrica).
24 spp. are listed from the locality (Slovenia). The proposed landscaping would destroy many important habitats and would probably trigger the local extinction of Lestes barbarus, L. dryas, L. virens vestalis, Aeshna affinis and Sympetrum meridionale. Additional research and construction of substitute habitats are suggested.
- (18952) BEDJANIČ, M., 2011. Projekt “Varstvo in upravljanje slakovodnih mokrišč v Sloveniji – WETMAN 2011-2015”. Popis začetnega stanja in raziskave vpliva projektnih aktivnosti na populacije kačjih pastirjev (Odonata): pilotno območje Mura-Petišovci (Mejnik 1). – [Project “Protection and management of freshwater wetlands in Slovenia – WETMAN 2011-2015”. Description of the initial stage and inquire into the effects of the activities of the Project on dragonfly populations (Odonata): pilot area Mura-Petišovci]. Bedjanič, for Zavod Republike Slovenije za varstvo narave, Ljubljana. 59 pp. (Slovene). – (Author: Kolodvorska 21/B, SI-2310 Slovenska Bistrica).
The objectives of the work were: (1) the inventarisation of the spp. occurring in the backwaters at Nagy Parlag, Muriša and Csiko Legelo (Prekmurje, NE Slovenia); – (2) assessment of the odon. populations status, particularly that of Aeshna viridis, Leucorrhinia caudalis and L. pectoralis; – and (3) the preparation of management suggestions for the 3 wetland areas, with emphasis on the above 3 spp.
- (18953) BEDJANIČ, M., 2011. Projekt “Varstvo in upravljanje sladkovodnih mokrišč v Sloveniji – WETMAN 2011-2015”. Popis začetnega stanja in raziskave vpliva projektnih aktivnosti na populacije kačjih pastirjev (Odonata): pilotno območje Pohorje (Mejnik 1). – [Project “Protection and management of freshwater wetlands in Slovenia – WETMAN 2011-2015”. Description of the initial stage and inquire into the effects of the activities of the Project on dragonfly populations (Odonata): pilot area Pohorje]. Bedjanič, for Zavod Republike Slovenije za varstvo narave, Ljubljana. 54 pp. (Slovene). – (Author: Kolodvorska 21/B, SI-2310 Slovenska Bistrica).
The objectives of the work were: (1) the inventarisation of the spp. occurring in the Klopnovrška, Lovrenska and the Javorski Vrh rised bogs (Pohorje, Slovenia); – (2) assessment of the odon. population status, particularly that of Aeshna juncea, Somatochlora arctica and Leucorrhinia dubia; – and (3) the preparation of management suggestions for the 3 wetland areas, with emphasis on the above 3 spp.
- (18954) BERNARD, R., M. HEISER, A. HOCHKIRCH & T. SCHMITT, 2011. Genetic homogeneity of the Sedgling Nehalennia speciosa (Odonata: Coenagrionidae) indicates a single Würm glacial refugium and trans-Palaeartic postglacial expansion. *J. zool. Syst. evol. Res.* 49(4): 292-297. – (First Author: Dept Gen. Zool., Mickiewicz Univ., Umultowska 89, PO-61-614 Poznań).
The phylogeographic structures of taiga spp. often support the hypothesis of E Palaeartic refugia for these taxa, but the phylogeographic structures of

- northern temperate and southern boreal bog spp. are still poorly understood. Therefore, the genetic diversity and differentiation of the stenotopic *N. speciosa* is here analysed across its trans-Palaeartic range by means of sequencing 2 mitochondrial gene fragments, 16S rRNA-ND1 and cytochrome c oxidase II. Only 4 single nucleotide polymorphisms were detected over the 1130 sequenced nucleotides. The low genetic diversity and differentiation and thus the lack of phylogeographic structure imply postglacial expansion from a single Würm-Ice Age refugium, most likely located in the Asian Far East, i.e. the Manchurian refugium. From here, the sp. could have colonized, during the postglacial, large parts of Palaeartic, incl. Europe.
- (18955) BÖNSEL, A. & M. FRANK, 2011. Eine Momentaufnahme von *Crocothemis erythraea* (Brullé, 1832) und *Aeshna affinis* Vander Linden, 1820 in der nordostdeutschen Jungmoränenlandschaft von Mecklenburg-Vorpommern (Odonata). *Ent. Nachr. Ber.* 55(1): 37-42. (With Engl. s.). – (First Author: Krähenberger Holz 8, D-18337 Marlow).
The current distribution of *C. erythraea* (32 localities, 7 with exuviae) and *A. affinis* (25 localities, 3 with exuviae) in Mecklenburg-Western Pomerania (E Germany) is summarised, mapped and discussed in terms of global warming.
- (18956) BRIX, K.V., D.K. DeFOREST & W.J. ADAMS, 2011. The sensitivity of aquatic insects to divalent metals: a comparative analysis of laboratory and field data. *Sci. total Envir.* 409: 4187-4197. – (First Author: EcoTox, 575 Crandon Blvd, 703 Key Biscayne, FL 33149, USA).
Based on literature, a summary is presented in a tab. of the acute metal toxicity data of cadmium, copper, lead, nickel and zinc for insects, incl. the odon., represented by a Zygoptera sp.
- (18957) CABANA, M., A. ROMEO & A. CORDERO, 2011. Primeiras citas de *Sympetrum flaveolum* (Odonata: Libellulidae) en Galicia. *Chioglossa* 3: 5 pp. [preprint]. – (First Author: Depto Biol. Animal, Fac. Cien., Univ. Coruña, Campus da Zapateira, ES-15071 A Coruña).
Records and observations (21 Aug.-19 Sept. 2010) from various sites at 6 localities; – Galicia, NW Spain.
- (18958) CHAKRAVORTY, J., S. GHOSH & V.B. MEYER-ROCHOW, 2011. Practices of entomophagy and entomotherapy by members of the Nyishi and Galo tribes, two ethnic groups of the state of Arunachal Pradesh (North-East India). *J. Ethnobiol. Ethnomed.* 2011, 7: 5, 14 pp.; – <http://www.ethnobiomed.com/content/7/1/5> – (Third Author: Sch. Engin. & Sci., Jacobs Univ., Research II, rm 37, D-28759 Bremen).
As edible are listed the larvae of *Enallagma*, *Ictinogomphus rapax*, *Stylurus*, *Brachythemis contaminata*, *Diplacodes*, *Pachydiplax*, *Sympetrum* and *Urothemis*. Among the therapeutic insects there are no odon.
- (18959) BULLETIN OF THE OREGON ENTOMOLOGICAL SOCIETY (ISSN none), Vol. 2011, Nos Spring, Summer & Fall 2011. (c/o J. Johnson, jt_johnson@comcast.net).
[Odonatol. notes]: [Spring]: *Lyons, R.*: Life in winter ponds along the coast (p. 3); – *Johnson, J.*: A new odonate for Oregon (*Ischnura barberi*, p. 6); – *Book announcements*: The dragonflies and damselflies of Oregon, by C. Kerst & S. Gordon; – A checklist of North American Odonata, by D.R. Paulson & S.W. Dunkle (p. 6); – [Summer]: *Lyons, R.*: Desert odonate hunt 2011 (pp. 2-5; records E Oregon); – *Johnson, J.*: Desert odonate trip, 17-19 June 2011: odonate species list (p. 6); – [Fall]: *Gordon, S.*: 2011 Oregon *Aeshna* blitz (pp. 1-3; records from Lane, Klamath and Douglas counties); – *Johnson, J.*: The brief history of *Paltothemis lineatipes* in Oregon (p. 3); – *Lyons, R.*: New county record for *Aeshna constricta* (pp. 4-5); – *Kerst, C.*: Pins to envelopes (p. 5).
- (18960) CARRIÇO, C., J.M. COSTA & T.C. SANTOS, 2011. Descriptions of the larva of *Neocordulia machadoi* Santos, Costa & Carriço, 2010 (Odonata: Corduliidae) from Brazil. *Biota neotrop.* 11(2): 3 pp.; – <http://www.biotaneotropica.org.br/v11n2/en/abstract?article+bn01511022011> (with Port. s.). – (First Author: Biol. Animal, Depto Biol., PPGBA, Univ. Fed. Rural Rio de Janeiro, BR-23890-000 Seropédica, Rio de Janeiro, RJ).
The larva is described and illustrated from the Eubosose stream, São Tomé das Letras (Minas Gerais, Brazil). This is the 8th known neotropical corduliid larva.
- (18961) CHERTOPRUD, M.W., 2011. Diversity and classification of rheophilic communities of macrobenthos in middle latitudes of European Russia. *Zh.*

- obshch. Biol.* 72(1): 51-73. (Russ., with Engl. s.). — (Dept Hydrobiol., Fac. Biol., Moscow Lomonosov St. Univ., Leninskie gory, Moscow-119992, Russia). Based on 450 samples from 115 streams, an attempt is made to describe the overall diversity of rheophilic communities dwelling on stream bottom and in macrophytes. In total, 39 community types were identified by the Braun-Blanquet method, their taxonomic and structural characteristics are described, the associations with the biotopes are outlined and a biotopical nomenclature is proposed. The communities are subdivided into 4 biotope classes, viz.: krenal (springs and spring brooks with mixed substrates), rhitral (stony and woody substrates), phythal (macrophytes) and pelal (soft ground). *Calopteryx splendens*, *Platycnemis pennipes*, *Gomphus vulgatissimus* and *Somatochlora metallica* are listed among the leading or accompanying spp. in the following biotopes, whose nomenclature was constructed in the traditional Greek style: limnophythal, pleistophythal, hyporheophythal, pelorheophythal, grassorheophythal, rhizorheophythal, palidorheophythal, hypoxyloribital and hypopelal. The effect of the spatial scale on the definition of communities is described along with the problems of the community dynamics.
- (18962) [DINGS, N.] DRIESSEN, I., 2011. "Pedigree". *Gemeentegids 2011-2012, Bergen*, p. 93. — (Foto Ingrid Driessen, Jeroen Boschstraat 20, NL-5854 CZ Bergen/Lb).
A photograph of the monument called "Pedigree", by Nicolas Dings, located at a rotunda of Hwy N271 in Well/Lb, the Netherlands. Among the represented animals there is a dragonfly.
- (18963) FLIEDNER-KALIES, T. & H. FLIEDNER, 2011. *Libellen im Kanton Schwyz*. Schwyz. naturf. Ges., Einsiedeln. 208 pp. [Ber. schwyz. naturf. Ges. 16]. Softcover (21.2 × 29.5 cm). ISBN 978-3-9523221-7-8. — (Publishers: Arvenweg 10, CH-8840 Einsiedeln).
A very thorough monograph on the odon. fauna (62 spp.) of canton Schwyz (Switzerland). The treatment of each sp. includes a brief description, sections on distribution, habitats, biology and the conservation status, with photographs of both sexes, a phenology graph and a distribution map. The introductory chapters are presenting an outline of the history of exploration of the odon. fauna of the canton and of general odon. biology, descriptions of odon. biotopes and information on the impact of climate change. The concluding chapter is devoted to odon. protection and conservation. An exhaustive regional bibliography is appended.
- (18964) HÄMÄLÄINEN, M., X. YU & H. ZHANG, 2011. Descriptions of *Matrona oreades* spec. nov. and *Matrona corephaea* spec. nov. from China (Odonata: Calopterygidae). *Zootaxa* 2830: 20-28. — (First Author: Sunankalliontie 13, FIN-02760 Espoo).
M. oreades sp. n. (holotype ♂: China, Gansu, Wenxian, Bikou, alt. 950 m, 9/13-VII-2005) and *M. corephaea* sp. n. (holotype ♂: China, Zhejiang, W Tianmushan, alt. 700 m, 8-VIII-2007) are described and illustrated for both sexes. The types are deposited at Inst. Ent., Life Sci. Coll., Nankai Univ., Tianjin, China. The 2 spp. differ markedly from the *M. basilaris*-group by their sparse venation and absence of bluish-white reticulation at the wing base.
- (18965) HAMASAKI, K., T. YAMANAKA, K. TANAKA, Y. NAKATANI, N. IWASAKI & D.S. SPRAGUE, 2011. Environmental characteristics accounting for Odonata assemblages in rural reservoir ponds in Japan. *Jpn agr. Res. Q.* 45(2): 187-196. — (First Author: Biodiv. Div., Natn. Inst. Agro-Exp. Sci., NIAES, Tsukuba, Ibaraki, 305-8604, JA).
To clarify the effect of environmental factors on odon. assemblages in rural reservoir ponds, a survey of adults was conducted during 3 sampling periods in 70 ponds in Ibaraki pref. Cluster analysis, indicator spp. analysis (INSPAN) and non-metric multidimensional scaling (NMDS) were used in combination to determine the relationship between odon. assemblages and biotic, physicochemical, and regional variables (the types of land use surrounding the ponds). A total of 41 spp. were recorded, 24 of these, excluding rare spp., were used for each analysis. The ponds were classified into 6 groups, and significant indicator spp. were selected from 4 of these groups. Examination of the correlation between each environmental variable and NMDS axes 1 and 2 revealed the profound effects of the presence of forest, paddy field, or open area around the ponds on the indicator spp. composition of each group. It was also revealed that the aquatic vegetation and forests around the ponds provide desirable conditions for the odon. and, in contrast, the concrete revetment has a detrimental effect. These results suggest that the recent decrease of forests around ponds and the reconstruction with the concrete revetment will have a negative effect on the odon. assemblages in ponds.

- (18966) HEIDECKE, H., 2011. Libelle des Jahres signalrot. *Mag. Bund Umwelt Naturschutz Dtl.* 2011(3): 6. – (Sieverstorstr. 56, D-39106 Magdeburg).
For 2011, *Crocothemis erythraea* was selected as „The dragonfly of the year” in Germany, since its increasing occurrence and distribution in Germany present an exceptionally good example of the recent climate change.
- (18967) HONKANEN, M., 2011. Perspectives on variation in species richness: area, energy and habitat heterogeneity. *Jyväskylä Stud. biol. envir. Sci.* 219: 1-46. [ISBN 978-951-39-4206-9]. Acad. Diss. Univ. Jyväskylä. (With Finn. s.). – (Dept Biol. Envir. Sci., P.O. Box 35, FIN-40014 University of Jyväskylä)
A chapter (pp. 26-27) is devoted to the odon. species richness. It is largely determined by the density of aquatic vegetation, but only few dragonflies depend directly on some specific plant spp. (e.g. *Aeshna viridis* on *Stratiotes aloides*). Additionally, water pH and shoreline length (or pond area) also have an effect on odon. species richness.
- (18968) KELLER, D., S. BRODBECK, I. FLÖSS, G. VONWIL & R. HOLDEREGGER, 2011. Ausbreitung und Besiedlungsgeschichte der Zierlichen Moosjungfer *Leucorrhinia caudalis* in der Schweiz (Odonata: Libellulidae). *Entomo helvetica* 4: 139-152. (With Engl. & Fr. s's). – (First Author: Eidg. Forschungsanstalt WSL, Zürcherstr. 111, CH-8903 Birmenstorf).
The dispersal and colonisation history of *L. caudalis* in Switzerland are outlined. The sp. was formerly widespread in the lowlands, but only a single known population was left in the 1980s. However, a spread has been observed in the 1990s, where close-by ponds at a distance of 0.5-7 km have been colonised. Additionally, 2 new populations at distances of 30 km and 50 km were discovered recently. In the present study, a combination of a mark-resight study with genetic methods was applied to investigate current migration and genetic footprints of colonisation history. Both the mark-resight and the genetic study showed that *L. caudalis* is a sedentary sp. that migrates only rarely, seldom exceeding distances of 5 km. The genetic results reflected the recent colonisation history. The oldest and largest population was genetically the most variable and acted as source for recent colonisations. The close-by but only recently founded populations also showed high genetic variability, implicating that close ponds are relatively easily colonised and establish well if functional connectivity is ensured.
- (18969) KIYOSHI, T., J.-i. TAKAHASHI, T. YAMANAKA, K. TANAKA, K. HAMASAKI, K. TSUCHIDA & Y. TSUBAKI, 2011. Taxonomic uncertainty of a highly endangered brook damselfly *Copera tokyoensis* Asahina, 1948 (Odonata: Platycnemididae), revealed by the mitochondrial gene genealogy. *Conserv. Biol.* 12: 845-849. – (First Author: Cent. Ecol. Res., Kyoto Univ., Hirano 2-509-3, Otsu, Shiga, 520-2113, JA).
In Japan, *C. tokyoensis* occurs sympatrically with the common *C. annulata*. Mitochondrial gene genealogy, reconstructed by the maximum likelihood method, showed that these 2 spp. are not reciprocally monophyletic. Possibly they might have experienced mitochondrial regressions through hybridizations. The effect of hybridization on the endangered sp. is poorly understood. Taxonomic uncertainty might also explain the situation, since the extremely dispersed pattern of the haplotype could not have originated in a single or 2 hybridizations. In the Kanto distr., 3 closely located *C. tokyoensis* populations show a significant population diversification. This might suggest the low dispersion tendency in this endangered sp.
- (18970) KOSIK, J., Z. ČADKOVA, I. PŘIKRYL, J. SEDA, L. PECHAR & E. PECHAROVA, 2011. Initial succession of zooplankton and zoobenthos assemblages in newly formed quarry lake Medard (Sokolov, Czech Republic). *In: Růde, Freund & Wolkersdorfer*, [Eds], *Mine water: managing the challenges*, pp. 517-522, IMWA, Aachen. – (First Author: Appl. Ecol. Lab., Fac. Agric., Univ. South Bohemia, České Budějovice, Czech Republic).
The quarry lake of Medard (near Sokolov, W Bohemia) is probably the largest of its kind in the Czech Republic. Coal mining was stopped in 2000, the mine water was pumped out in 2010 and (mainly) river water is coming into it now. At present (first half of 2011), 8 odon. spp. occur there.
- (18971) LeGRAND, H.E. & T.E. HOWARD, Jr, 2011. *Notes on the odonates of North Carolina. Third approximation.* 194 pp. – (First Author [Species accounts]: NC Natural Heritage Program, 1601 MSC, Raleigh, NC 27699-1601, USA; – Second Author [Website administrator]: 701 Park St., Fuquay-Varina, NC 27526, USA).
County distribution maps and adult phenology graphs, with the information on distribution and abundance in the state, flight periods, habitats, behav-

- our, and various additional comments. The work is intended to serve as a "handbook on North Carolina odonates (USA).
- (18972) LEHMANN, F.-O., 2011. The mechanisms of lift enhancement in insect flight. *Naturwissenschaften* 91: 101-122. – (BioFuture Res. Gr., Dept Neurobiol., Univ. Ulm, Albert-Einstein-Allee 11, D-89081 Ulm).
A review paper.
- (18973) *Die LIBELLENGRUPPE DER ORTSGRUPPE HERBRUCK INFORMIERT*, 2011. Bund Naturschutz Bayern 2011(1).
Loos, G.: Libellen mit Migrationsuntergrund im Landkreis Nürnberger Land (pp. 1-13); – *Schroth, K.*: Die Glänzende Binsenjungfer [*Lestes dryas*] im FFH Gebiet bei Reichenschwand (pp. 14-17).
- (18974) LIEBELT, R., M. LOHR & B. BEINLICH, 2011. Zur Verbreitung der Gestreiften und der Zweigestreiften Quelljungfer (*Cordulegaster bidentata* und *C. boltonii*) im Kreis Höxter (Insecta, Odonata, Cordulegastridae). *Beitr. Naturk. Egge Weser* 22: 3-18. – (First Author: Altes Forstamt 1, D-37691 Boffzen).
The distribution of the 2 spp. in the district of Höxter (NRW, Germany) is outlined and the required protection measures of their habitats are proposed.
- (18975) MEURGEY, F. & C. POIRON, 2011. The true *Dythemis multipunctata* Kirby, 1894, from the West Indies and proposed new taxonomic status (Odonata: Anisoptera: Libellulidae). *Zootaxa* 3019: 51-62. – (Mus. Hist. Nat., 12 rue Voltaire, F-44000 Nantes).
The true *D. multipunctata* is illustrated and the ♀ is described for the first time based on specimens from the type locality, St Vincent (Lesser Antilles). The taxonomic status of the sp. is discussed, and notes on behaviour, habitat, and distribution range are provided. *D. multipunctata* is to be considered a ssp of *D. sterilis* (Hag.) and mainland populations, previously known as *multipunctata*, are now to be called *D. nigra* Martin.
- (18976) MORENO PALLARES, M.I., 2011. *Distribución especial y temporal de las comunidades de náyades de odonatos en los humedales La Vaca y Santa María del Lago, Bogotá, Colombia*. Acad. Diss., Depto Biol., Fac. Cien., Univ. Nac. Colombia, Bogotá. 56 pp.
The analysis of spatial and temporal variation in the communities of *Enallagma civile*, *Ischnura cruzi*, *Mesamphiagrion laterale* and *Rhionaeschna marchali* larvae in the wetlands of La Vaca and Santa María del Lago (Bogotá, Colombia) is presented with reference to the environmental conditions.
- (18977) MÜLLER, J. & R. STEGLICH, 2011. Fundort- und Artenliste eigener Libellen-Nachweise (Odonata) in Sachsen-Anhalt für die Jahre 2009 und 2010. *Halophila* 54: 15-19. – (First Author: Frankefelde 3, D-39116 Magdeburg).
The 2009 and 2010 records from Sachsen-Anhalt (Germany).
- (18978) NELSON, B., C. RONAYNE & R. THOMPSON, 2011. *Ireland Red List No. 6: Damselflies and dragonflies (Odonata)*. Natn. Parks & Wildl. Serv., Dept Envir., Heritage & Local Government, Dublin. iv + 27 pp. – (First Author: Natn. Parks & Wildl. Serv., Ely Pl., Dublin-2, Eire).
Based on almost 32,000 records, 24 spp. are evaluated for their conservation status using the IUCN criteria (2001, 2003). *Lestes dryas* is assessed as Near Threatened (NT), *Coenagrion lunulatum* and *Ischnura pumilio* are Vulnerable (VU), and *Cordulia aenea* and *Somatochlora arctica* are Endangered (EN).
- (18979) NELSON, S.M., 2011. Response of stream macroinvertebrate assemblages to erosion control structures in a wastewater dominated urban stream in the southwestern U.S. *Hydrobiologia* 663: 51-69. – (Techn. Serv. Cent., Bureau Reclamation, Denver Fed. Cen., Bldg 56, Rm 2010, P.O. Box 25007, Denver, CO 80225, USA).
The study was conducted (2000-2009) in a wastewater dominated drainage in Las Vegas (Nevada, USA). The pollution and sediment tolerance values are given (familywise) for Coenagrionidae, Calopterygidae, Aeshnidae, Gomphidae and Libellulidae.
- (18980) NESEMANN, H., R.D.T. SHAH & D.N. SHAH, 2011. Key to the larval stages of common Odonata of Hindu Kush Himalaya, with short notes on habitats and ecology. *J. threatened Taxa* 3(9): 2045-2060. – (First Author: Cent. Envir. Sci., Central Univ. Bihar, BIT Campus, Patna, Bihar-800014, India).
A family key to the larvae from various parts of Nepal and northern India is presented, and the morphology, biology and habitats are familywise

- described, supported by illustrations of the typical representatives.
- (18981) OLTHOFF, M., K. HANNIG, K. WITTJEN & T. ZIMMERMANN, 2011. Biologische Vielfalt auf dem Truppenübungsplatz Borkenberge. *Natur Nordrhein Westfalen* 2011(3): 37-41. — (First Author: Naturschutzzentrum Coesfeld, Borkener Str. 13, D-48653 Coesfeld).
Includes a presentation of highlights in the odon. fauna of the military training area of Borkenberge (North Rhine-Westphalia, Germany). *Ceragrion tenellum*, *Somatochlora arctica* and *Orthetrum coerulescens* are among the noteworthy autochthonous spp. *Leucorrhinia pectoralis* also probably breeds in the area.
- (18982) ORLANDI BONATO, K., 2011. *Estudo da comunidade, dieta e efeitos de variáveis físicas ambientais sobre a taxocenose de peixen em um riacho litorâneo*. Diss Pós-Graduação Ciên. Biol.-Zool., Univ. Fed. Paraná, Curitiba. xv + 99 pp. (Port., with Engl. s.). — (Author's address not stated).
The stomach contents were analysed of 20 fish spp. from the Sambaqui basin (Morretes, Paraná, Brazil), most of them pertaining to the Siluriformes. Along with the filamentous algae, diatoms and larval Chironomidae and Ephemeroptera, odon. larvae were among the principal diet items. The diet inventories per fish sp. are not provided.
- (18983) OTT, J. & N. HOFFER, not dated, received 2011. *Wie helfe ich einer Libelle? Lebensweise und Schutz der Libellen*. Bund für Umwelt und Naturschutz Deutschland, Berlin. Not paged, 14 pp. ISBN none. — (Publishers: Am Köllnischen Park 1, D-10179 Berlin).
A brochure, directed at the widest readership, presenting briefly the most essential information on dragonflies and their importance as bioindicators, with emphasis on protection and conservation.
- (18984) PALACINO-RODRIGUEZ, F., 2011. *Taxonomy and phylogeny of the genus Erythemis Hagen, 1861 (Odonata: Libellulidae)*. Thesis Magister en Ciencias, Univ. Nac. Colombia, Bogotá. 141 pp. (Span., with Engl. s.). — (Author: Inst. Cien. Naturales, Univ. Nac. Colombia, A.A. 7495, Bogotá, Colombia).
In order to cover the intra- and interspecific variability and to define phylogenetic relationships within the genus, additional structural characters are proposed, all taxa are keyed and the phylogenetic relationships are analysed. The characters are assessed using multivariate approaches such as the Principal Component Analysis, and discriminant analysis. For phylogenetic analysis the parsimony method was used, including the outgroup spp. of the genera *Libellula*, *Miathyria*, *Pantala*, *Perithemis*, *Rhodopygia* and *Sympetrum*.
- (18985) PEREZ-GELABERT, E., R.H. BASTARDO & S. MEDRANO, 2011. Entomofauna del Parque Nacional Loma Nalga de Maco y alrededores, provincia Elias Piña, Republica Dominicana. *Novit. caribaea* 2011(4): 80-90. (With Engl. s.). — (First Author: Dept Ent., US Natn. Mus. Nat. Hist., Smithsonian Instn, P.O. Box 37012, Washington, DC 20013-7012, USA).
Based on literature, 8 odon. spp. are listed from the Park and its surroundings, Dominican Republic.
- (18986) POPOOLA, K.O.K. & A. OTALEKOR, 2011. Analysis of aquatic insect communities of Awba reservoir and its physico-chemical properties. *Res. J. Envir. Earth Sci.* 3(4): 422-428. — (Dept Zool., Univ. Ibadan, Ibadan, Oyo, Nigera).
The reservoir is located at the Univ. of Ibadan (Nigera), alt. 185 m. The occurrence at 3 sampling stations is familywise shown for 3 odon. fam. A list of spp is not provided.
- (18987) QIAN, C., Z.-m. WANG & D.-f. ZHAO, 2011. New records of Odonata in the Northeast area and Jilin province in China. *J. Jilin agric. Univ.* 33(2): 169-171, 184. (Chin., with Engl. s.). — (Coll. Agron., Jilin Agric. Univ., Changchun-130118, China).
Records of 6 spp.
- (18988) REMSBURG, A., 2011. Relative influence of prior life stages and habitat variables on dragonfly (Odonata: Gomphidae) densities among lake sites. *Diversity* 3: 200-216. — (Unity Coll., 90 Quaker Hill Rd, Unity, ME 04988, USA).
The study was conducted (2005, 2006) at 22 sites on 11 lakes in Vilas co. NE Wisconsin (USA). 6 spp. were involved, *Gomphus spicatus* was dominant. Generally, water quality conditioned larval densities and riparian wetland vegetation those of emerging adults. Adult densities from the previous season helped to predict densities of early instar larvae, suggesting that oviposition site selection controlled the local larval distribution more than their survivorship or

movement. Late instar densities helped to predict the densities of emerging adults, suggesting that variation in survivorship of final instar larvae among sites is small relative to the variation in larval recruitment.

- (18989) REN, G.-d. & J. NING, 2011. Differentiation and phylogeny of metathoracic pleural sclerites in selected pterygote insects. *Entomotaxonomia* 33(2): 81-93. (Chin., with Engl. s.). – Coll. Life Sci., Hebei Univ., Boading, Hebei-071002, China).
The development of morphological characteristics in metathoracic pleural sclerites was analyzed in the representatives of 12 pterygote orders and a cladogram is produced. It indicates that Palaeoptera and Neoptera are clearly separated. Ephemeroptera are distantly related to Neoptera, while Odon. have a closer relationship. The systematic status and the evolutionary relationships of Neoptera are discussed and some arguments are provided that are in conflict with the current classification system.
- (18990) ŠÁCHA, D., 2011. *Ecofaunistic evaluation of dragonfly assemblages at the sites of European and national significance in northern Slovakia*. Diss., Fac. Nat. Sci., Comenius Univ., Bratislava. 205 pp., Annexes excl. (Slovak, with Engl. s.). – (Author: Podtatranského 31, SK-031-01 Liptovský Mikuláš). All available records from 251 localities in northern Slovakia are reviewed and revised. Out of the 62 spp., the information on the occurrence of *Coenagrion pulchellum*, *Nehalennia speciosa*, *Aeshna caerulea* and *Gomphus vulgatissimus* is unreliable and *Cordulegaster boltonii* is removed from the regional list. Information is presented on adult phenology and on the association of spp. with the type of habitats. In addition, a regional Red List is proposed.
- (18991) ŠÁCHA, D., 2011. New records of dragonflies (Insecta: Odonata) of mountain ranges in Liptov and Špis regions. *Folia faunist. slovakia* 16(2): 109-114. (Slovak, with Engl. s.). – (Podtatranského 31, SK-031-01 Liptovský Mikuláš).
Records of 22 spp., among which those of *Aeshna subarctica*, *Somatochlora alpestris* and *Sympetrum fonscolombii* are of particular interest.
- (18992) SCIBERRAS, A., 2011. First record of a successful breeding of *Anax ephippiger* Burmeister, 1839 in the Maltese Islands (Insecta, Odonata). *Naturalista sicil.* (IV) 35(2): 157-162. (With Ital. s.). – (131 'Arnest', Arcade St., Paola, Malta).
- A teneral ♂ (il-Qammieh, 23-VIII-2010) is brought on record, suggesting the sp. breeds on the Maltese Islands.
- (18993) SESTERHENN, T.M., 2011. Effects of predators and injury over different time scales in the damselfly *Ischnura posita* (Odonata: Coenagrionidae). *Ann. ent. Soc. Am.* 104(2): 358-363. – (Dept Biol., Univ. Kentucky, Lexington, KY 40506-0225, USA).
Sublethal appendage injury or loss has been shown to alter many behaviours of animals, including foraging and predation avoidance. But most studies of this phenomenon to date have been short-term in scope, and longer term studies may produce different results as seen in some studies on predator effects. Larval Zygoptera routinely autotomize their caudal lamellae and encounter predators, making them ideal for comparisons of short-term and longer term effects of appendage loss and predator exposure. In this study, activity and foraging of larval I. *posita* were examined, testing for effects of lamella loss and predator cues both in the short term (1 h) and the longer term (8 d). It was predicted that both predators and injury would decrease activity and foraging for a short time and that these effects would diminish over time. Results indicated that only the most severe injuries affected foraging, delaying first prey capture when no predator was present; but injury did not affect total prey caught. In the 1-h experiment, damselflies had lower activity in the presence of predator cues, with no effect of injury, whereas the 8-day experiment showed no effect of predator cues on activity. A major effect of injury or predator cues on activity or foraging of larval *Ischnura* was not found, and no effects were detectable over the entire 8-d study. It is concluded that the ecological implications of such injuries in nature may often be negligible.
- (18994) SMITH, I.M., E.E. LINDQUIST & V. BEHAN-PELLETIER, 2011. Mites (Acari) of the Montane Cordillera Ecozone. In: G.G.E. Scudder & I.M. Smith, [Eds], *Assessment of species diversity in the Montane Cordillera Ecozone*, pp. 1-76, R. Brit. Columbia Mus., Victoria. – (Cent. Experimental Farm, Biosyst. Res. Inst., Agric. & Agri-Food Canada, Ottawa, ON, K1A 0C6, CA).
Among the over 3000 spp. of mites conservatively estimated to occur in the Montane Cordillera Ecozone, there are 17 known *Arrenurus* (s.s.) spp. (incl. 2 undescribed spp.) the larvae of which are parasites on Odon.

- (18995) STANICZEK, A.H., 2011. Focus on aquatic insects. In: P. Bouchet, H. Le Guyader & O. Pascal, [Eds], *The natural history of Santo*, pp. 251-257, Mus. Natn. Hist. Nat., Paris; ISBN 978-2-85653-627-8. – (Author's address not stated).
A commented list of 17 odon. spp. known from the Pacific island of Santo, including references to their occurrence in New Caledonia, the Loyalties and Vanuatu.
- (18996) [TROCKUR, B. et al.] LILLIG, M., 2011. Atlas der Libellen, von B. Trockur et al. *Umweltmag. Saar* 2011(2): 35. – (c/o Dr B. Trockur, Schulstr. 4, D-66636 Tholey-Scheuren).
A book review of the work listed in OA 18829 and an interview (portrait incl.) with Dr B. Trockur.
- (18997) VAN DER WEIJDEN, H., 2011. Groene glazenmaker voor de rechtbank. – [Aeshna viridis at the court]. *Natura, Amst.* 108(5): 26-27. (Dutch). – (Author's address not stated).
The long and time-consuming legal way is described which finally led to a positive jurisdiction on the conservation of *Aeshna viridis* habitats in the Reeuwijkse Plassen in the city of Gouda area (the Netherlands).
- (18998) WU, C. & A.-h. ZHANG, 2011. Catalogue and geographical distribution of Odonata from Beijing. *J. Beijing Univ. Agric.* 26(3): 15-19. (Chin., with Engl. s.). – (Coll. Plant Sci. & Technol., Beijing Univ. Agric., Beijing-102206, China).
A list of 62 spp. collected (2008-2010) from the downtown parks and 8 wetland areas in the city of Beijing (China). The Palaearctic spp. constitute 53.2% of the fauna.
- (18999) ZABŁOCKI, P. & M. WOLNY, 2011. First record of *Anax ephippiger* (Burmeister) (Odonata: Aeshnidae) for the Opolskie Voivodship (SW Poland). *Forum faunistyczne* 1(1): 35-38. (Pol., with Engl. s.). – (Dział Przyn. Muz., Leśnicka 28, PO-47-154 Góra Św. Anny).
1 ♂, Grabówka village, 13-VII-2011; – Opole, Silesia (Poland).
- (19000) ZAIKA, V.V., 2011. *Fauna i naselenie amfibi-ontnykh nasekomykh (Insecta, Ectognatha: Ephemeroptera, Plecoptera, Trichoptera, Odonata) vodnykh potokov Altae-Sayanskoy gornoy oblasti.* – [Fauna and populations of aquatic insects (Insecta, Ectognatha: Ephemeroptera, Plecoptera, Trichoptera, Odonata) of watercourses in the Altay-Sayansk Upper district]. Autoreferat Dr Diss. Biol. Nauk, Tuvi. Inst. Kompleksnogo Osvoeniya Prirodnih Resursov, Sib. Otdel. Russ. Akad. Nauk, Kyzyl. 40 pp. (Russ.). – (Available at: Nauch. Biblioteka GOU VPO, Tomsk Gos. Univ., Prosp. Lenina 36, RUS-634050 Tomsk).
The study area is located in N Mongolia, ca 200 km N of the Baikal Lake (Russia). 24 odon. spp. are listed from the Tee-Ham river basin, and the Author's complete bibliography related to the subject of the dissertation is appended.
- (19001) ZHANG, H.-j., 2011. Study on *Gynacantha* genus (Odonata: Aeshnidae) from China. *J. Anhui agric. Sci.* 39(13): 7562-7564. (Chin., with Engl. s.). – (Shaanxi Bioresour. Key Lab., Shaanxi Univ. Technol., Hanzhong, Shaanxi-723000, China).
Notes on distribution and an illustrated key are presented for 9 spp.

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- (19002) DOW, R.A., Y.F. NG & C.Y. CHOONG, 2012. Odonata of Sungal Bebar, Pahang, Malaysia, with four species recorded for the first time from mainland Asia. *J. threatened Taxa* 4(3): 2417-2426. (With Bahasa Melayu s.). – (First Author: Naturalis, P.O. Box 9517, NL-3200 RA Leiden).
50 spp., collected in Sept. 2009 from Pekan Forest Reserve, SW Pahang, Penin. Malaysia, are brought on record. *Amphicnemis bebar* and *A. hoisen* are new for the region, and *Elatoneura coomansi*, *E. longispina*, *Brachygonia Ophelia* and *Tyriobapta laidlawi* are for the first time recorded from the Asian mainland.
- (19003) DIDHAM, R.K., T.J. BLAKELY, R.M. EWERS, T.R. HITCHINGS, J.B. WARD & M.J. WINTERBOURN, 2012. Horizontal and vertical structuring in the dispersal of adult aquatic insects in a fragmented landscape. *Fundam. appl. Limnol.* 180(1): 27-40. – (First Author: Sch. Anim. Biol., Univ. E. Australia, 35 Stirling Hwy, Crawley, WA 6009, AU).
The passive flight interception traps were deployed at ground and canopy levels in the Hope river fragmented forest (Southern Alps, New Zealand; alt. 600-1300 m). Two thirds of adult aquatic insects (Ephemeroptera, Plecoptera, Trichoptera, Megaloptera, Odon. [represented by *Austrolestes colenonis*]) were captured in the forest canopy rather than at ground level. Since the long-distance dispersal of

- aquatic adults is rarely observed, they may disperse through forest canopy and well above ground level.
- (19004) FRASER, F.C., 2012. *Handbooks for identification of British insects*, 10: *Odonata*. R. Ent. Soc., London. 49 pp. – (Author deceased in 1963). A reprint of the work first published in 1949, 2nd edn in 1956. – For Fraser's complete bibliography, see OA 6610.
- (19005) JAFFAR, A.R., 2012. Observations on the dragonfly *Camacinia gigantea* (Brauer) at the Night Safari, Singapore (Insecta: Odonata: Libellulidae). *Nature Singapore* 5: 7-11. – (Night Safari, 80 Mandai Lake Rd, Singapore-729826, Singapore). *C. gigantea* is considered rare in Singapore, where it was known from Bukit Timah Nature Reserve, Bukit Batok Nature Park, and from Sungei Buloh Wetland Reserve; the locality at Night Safari is new. The mating and oviposition behaviour are described.
- (19006) NGIAM, R.W.J. & T.M. LEONG, 2012. Larva of the phytotelm-breeding damselfly, *Pericnemis stictica* Selys, from forests in Singapore (Odonata: Zygoptera: Coenagrionidae). *Nature Singapore* 5: 103-115. – (First Author: Natn. Biodiv. Cent., Natn. Parks Board, 1 Cluny Rd, Singapore-259569, Singapore). The larvae were collected from tree holes in the Bukit Timah Nature Reserve and reared to the adult. The larva is here described and illustrated for the first time, and it is compared with that of *P. triangularis*. The habitat is also described in detail.
- (19007) RICHARDSON, A., 2012. Assessment of locations of refugia for ancient and relictual invertebrate fauna within the proposed ENGO forest conservation areas. *IVG Forest Conserv. Rep.* 3A: 1-17 – (Sch. Zool., Univ. Tasmania, P.O. Box 252-C52, Hobart, TAS 7001, AU). *Hemiphlebia mirabilis*, *Synthemiopsis* and *Archipeptalia* are considered; – Tasmania, Australia.

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COWLEY, J., 1935. Remarks on the names of some odonates. *Entomologist* 26: 154-156.

FRASER, F.C., 1957. *A reclassification of the Odonata*. R. zool. Soc. N.S.W., Sydney.

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