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Odonata of the great Lake Tonle Sap of Cambodia, as examined in 2017-2019

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Abstract

Lake Tonle Sap in NW Cambodia is the largest freshwater lake in Southeast Asia and one of the most productive freshwater ecosystems in the world, so its banks are a home for ca 1,5 million people. It serves as a natural reservoir of the excess water of the Mekong River and cyclically changes its area from 2,500 km^2 in May to 16,000 km^2 in October. Its banks are naturally occupied by temporarily inundated forest and scrub, at present mostly replaced by rice fields. The present day semiaquatic vegetation of the lake is to a large extent formed by invasive plant species. The hitherto existing data on Odonata of the lake are very scarce. The author briefly examined the bank and floodplain at the NW part of the lake in February/March 2017, June and November 2018 and December 2019. Five main localities studied are described and illustrated in detail. In total 41 odonate species of four families (22 in Libellulidae) were found. Most of them are common and widespread lentic species but *Macrogomphus phalantus* is a species hitherto known only by few specimens from swamped forests of Borneo and Sumatra; its Tonle Sap population was earlier described by the author as the subspecies *M. phalantus jayavarman* Kosterin, 2019. The earlier published report by Seehausen et al. (2016) of *Sinictinogomphus clavatus* (not found by the author) was a considerable extension of the known species' range to the south. Six species were found in all main examined localities and ten only in one of them. At any season at the lake immediate bank (that is water front at the lowest level), *Brachythemis contaminata* predominates overwhelmingly, *Orthetrum sabina* and *Crocothemis servilia* are numerous, two damselfly species, *Pseudagrion microcephalum* and *P. rubriceps*, invariably occur at floating vegetation (mostly water hyacinth), and *Trithemis pallidinervis*, *Urothemis signata*, *Rhyothemis phyllis*, *R. variegata* and *Tholymis tillarga* are common at bushes. *Agriocnemis nana, Ceriagrion praetermissum, Ischnura senegalensis, Macrogomphus phalantus, and Aethriamanta aethra* were occasionally met at the lake bank. Other 26 species were found, with different occurrence and quantity, on the lake floodplain. Variation of the male occiput coloration of *Amphiallagma parvum* is commented.

Key words: Odonata, dragonflies, damselflies, fauna, Cambodia, Lake Tonle Sap, Tonle Sap River, Mekong River, Siem Reap Province, Battambang Province, floodplain, temporarily inundated forest, *Amphiallagma parvum*

Figure 1. Lake Tonle Sap in a cosmic image at Google Earth.

Introduction

In its headwaters, the great Mekong River collects a big share of moisture brought by the summer monsoon to the Sino-Tibetan Mountains bordering from the east the huge Tibet Upland. Having left these mountains, the Mekong River flows to the south through southern China, provides the border between Myanmar and Laos, enters Laos, provides the border between Laos and Thailand, re-enters Laos, enters Cambodia and then enters Vietnam where falls to the Gulf of Siam of the South Chinese Sea. Being the seventh longest (4,350 km) river in Asia, with the catchment area of 795,000 km^2, it has been carrying a huge amount of sediments which made the sea to step back and formed the alluvial Cambodian Lowland which once was a bay of the Gulf, so that in its lower reaches Mekong has to pass through its own flat alluvium. This lowland is situated almost at the sea level and is so flat that Mekong at its higher levels fails to discharge all its water to the sea. The excess water is therefore redirected and stored in the natural reservoir of Lake Tonle Sap (Khmer 'big lake of fresh water') situated in the centre of the Cambodian Lowland (Fig. 1). It is connected with Mekong by the Tonle Sap River which joins it at the city of Phnom Penh, the capital of Cambodia (Fig. 1). During the summer monsoon, from May to September, this river flows from Mekong to fill Lake Tonle Sap. When the Mekong level decreases, the current reverses and the water stored in Lake Tonle Sap starts to flow back to Mekong, to be at last discharged to the sea. Hence the Tonle Sap River changes its direction twice a year, approximately in late May-early June and late October-early November, and the Cambodian New Year celebrated on 14-16th of April is associated with its spring turn (although currently takes place somewhat ahead of this). As a result, Lake Tonle Sap cyclically changes its length of 160 km, the area of 2,500 km^2 (Fig. 2), the

volume of 1 km^3, and the average depth of 1 m in May to a length of 250 km, the area of 16,000 km^2, the volume of 80 km^3, and an average depth of 6-9 m in October (Mekong River Commission 2005). However, Eddie Smith (pers. comm.) informed me that in recent decades the lake seasonal maxima became smaller than this. The lake is also fed by its NW tributary, the Stung Sangkae (or Sankar) River. Sounding has shown that the lake bottom is perfectly flat without any relief, with the deepest point situating just 2.4 m above sea level (E. Smith, pers. comm.). In these respects, Tonle Sap is somewhat analogous to the Amazon River or even the epicontinental seas of the Mesosoic.

Figure 2. Lake Tonle Sap at its high level inundating the flatland surrounding its NE end at Kampong Chhnang Town. Photos by Eddie Smith.

Nevertheless it is fairly young, as formed just 6-8 thousand years ago, that is rather shortly after the Holocene onset, obviously following the increase of humidity at higher latitudes and the volume of the Mekong flow.

Tonle Sap is the largest freshwater lake in Southeast Asia and one of the most productive freshwater ecosystems in the world. Like the Nile in Egypt, this huge fluctuating water body full of fertile sediments has always been the source of living resources (Fig. 3), through rice farming and fishing (the latter practiced by Cham rather than Khmer people), for 1.2-1.3 million people populating its banks (but in the fishing season lasting from October to June, their number increases to 1.4-1.6 million). This was a prerequisit of the rise of the famous Angkorian Civilisation in IX century, whose capital was the largest urban centre in the world in XI-XIII centuries. At present the water surface (Figs 4-5), as well as seasonably flooded forest, is adorned with numerous large, arrow-shaped fish traps and speckled with floating villages (Figs 6-7). On the surrounding flatland, several embankments go parallel to the water front, so that when the lake shrinks, shallow water (partly supplied also with channels from outside the lake) is retained at their inland side and is subsequently used for watering rice field at their lake-faced side. As a rule these shallow 'reserves'

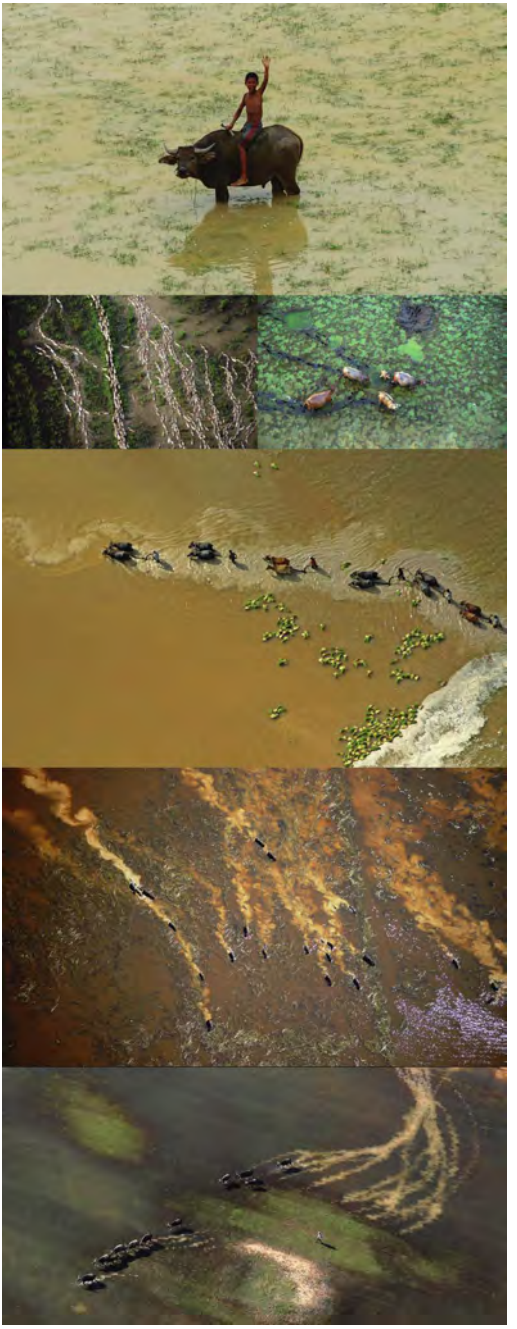


Figure 3. Water buffaloes and ducks (left near the top) in shallow waters at the Lake Tonle Sap banks. Photos by Eddie Smith.

are covered with thick but low temporarily inundated scrub, but at least a huge area (some 3 x 2 km) SW of Siem Reap City, bordered by a road embankment going from Phnom Krom village to Sambuor village, is a deeper and permanent lotus/water hya-

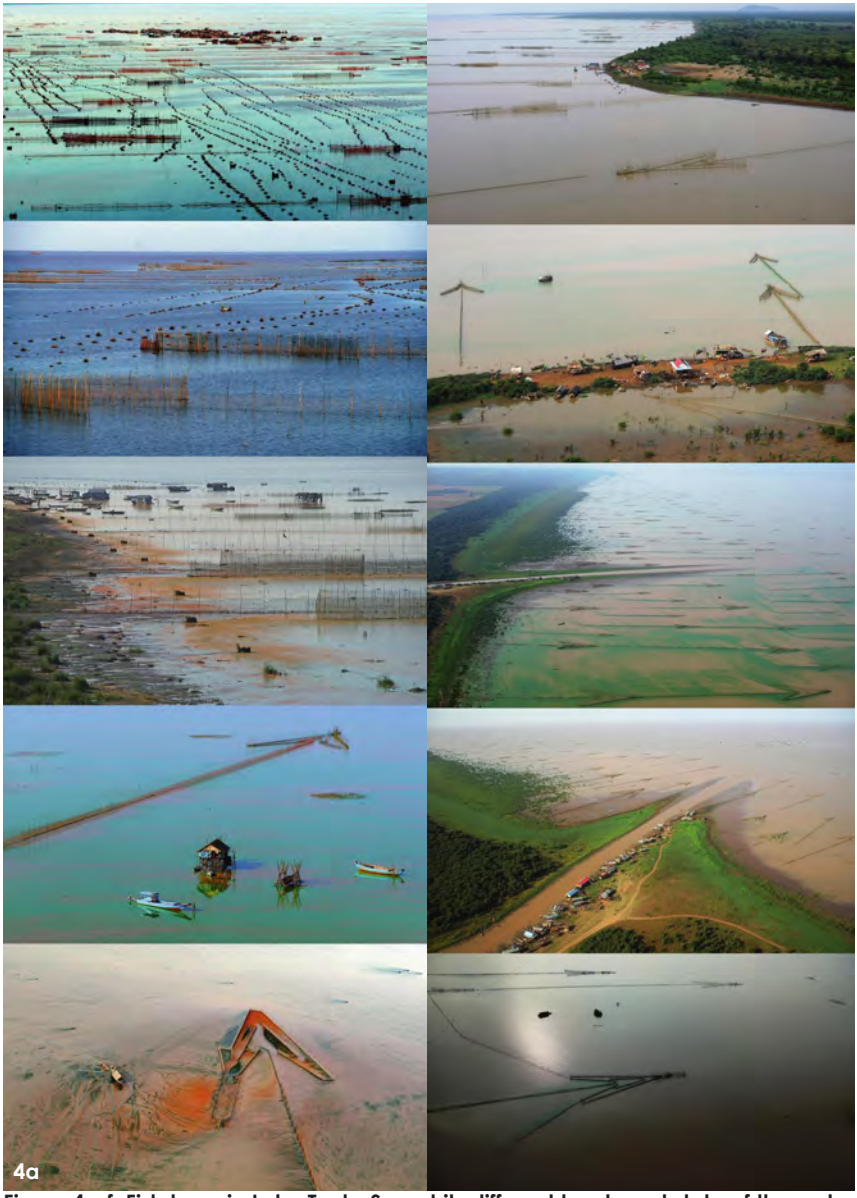


Figure 4a-f. Fish traps in Lake Tonle-Sap at its different levels and state of the water. Photos by Eddie Smith.

cinth swamp. This wetland-creating practice provides good habitats of many wetland birds, first of all Asian openbill storks (*Anastomus oscitans* (Boodayert, 1783) (Fig. 8). Beside these regular flat reserves formed by dams parallel to the lake bank, small deeper and roundish water reserves are scattered here and there (Fig. 9); these are mostly illegal and are regularly destroyed by the local authorities.

The natural vegetation of Lake Tonle Sap banks was the peculiar, temporarily flooded forest composed mostly of *Barringtonia acutangula* (L.) Gaertn., *Dyospiros* sp. and *Terminalia cambodiana* Gagnep. (L. Everaere pers. comm.). This forest has been depleteds because of human overexploitation lasting for at least one thousand year but remains at the lowermost reaches and the mouth of the Sangkae River, along the southern bank and in certain refugia on the northern bank, e.g. in popular touristic sites of the villages of Kampong Pluk and Kampong Khleang (see relevant sections below). In the remote past, the lake banks would have abounded in crocodiles, elephants, rhinos, wild water buffaloes etc. but at least a thousand years of thriving human civilisation (that is lasting for a considerable part of the lake age) left no room for them. Yet the lake is still almost the last refugium of the Mekong Giant Catfish (*Pangasianodon gigas* Chevey, 1931), one of the largest freshwater fishes in the world.

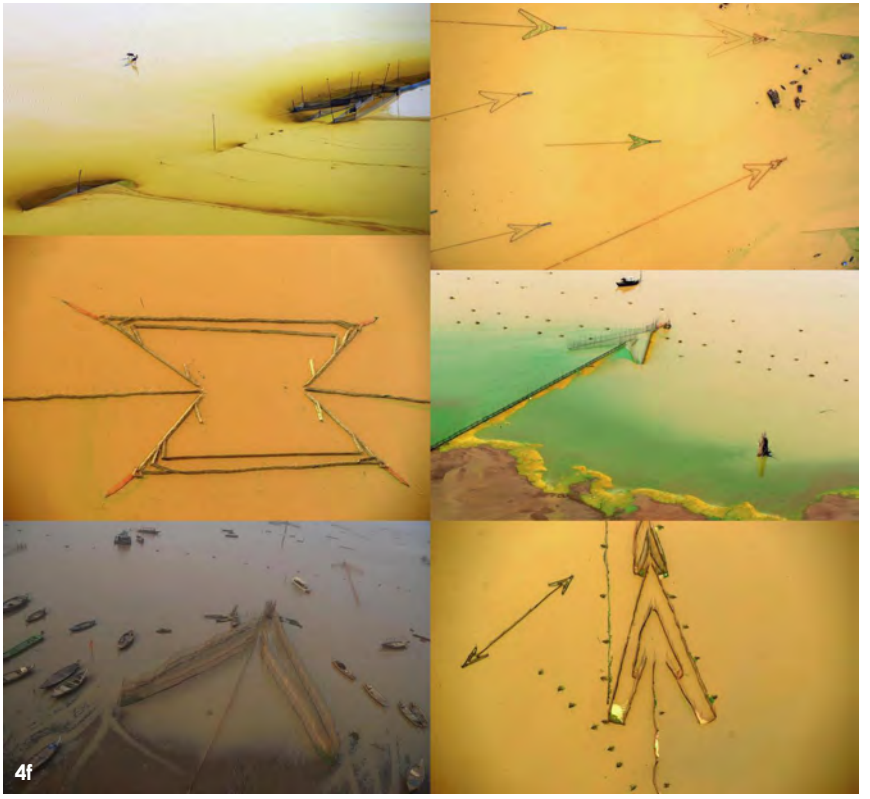
However special the Tonle Sap ecosystem is, it is currently far from its pristine state not only because of deforestation, extermination of large animals and overexploitation if natural resources but also, if not mainly, due to the prolonged history of alien species invasion. Thus, large areas of the shallow water surface in inundated forest and scrub is covered by carpets (Fig. 10) of Water Hyacinth (*Eichhornia crassipes* (Mart.) Solms), an invasive species of the Amazonian origin, which produces enormous biomass and comprises an overwhelming majority of floating vegetation. Among the water hyacinth, rosettes are frequent of the Water Cabbage (*Pistia stratiotes* L.), another species of probably American origin. The inner zone of seasonably flooded scrub facing the lake bank is largely formed by the 'Giant Sensitive Tree' (*Mimosa pigra* L.),

a tall semiaquatic spiny bush of a Mexican origin, and side-by-side with it Giant Cane (*Arundo donax* L.) emerges from water, whose indigenous range probably was in the Mediterranean and Near East, while both are interspersed with floating water hyacinth (Fig. 11). Hence most of the bank vegetation below tree level is currently formed by alien species. In low water season, the once inundated tree branches up to 3-4 m above the emerged ground are speckled by dry dead colonies of two species of bivalve mollusks from the family Mytilidae (Fig. 12), *Synomytilus harmandi* (Rochebrune, 1882) and *Limnoperna fortunei* (Dunker, 1856), of which the former is the Mekong catchment endemic while the latter is thought to have invaded Indochina from

China (Morton & Dinesen 2010). The actual alteration of the Tonle Sap ecosystem by invasive species may be much more profound than is noticeable by superficial observations.

Also there is a furiously debated plan (financed by Chinese money) to construct a large hydropower dam across Mekong in Kratie Province. It would regulate Mekong and is expected to stop the Tonle Sap level cycle, thus destroying its unique ecosystem and depriving about million people from living resources.

Surprisingly for such a unique and at the same time imperiled wetland, hitherto there was no special study of Odonata of Lake Tonle Sap, probably because of poor faunistic expectations. Occasional data were published by Benstead (2006), Roland & Roland (2010), Roland et al. (2011) and Seehausen et al. (2016). All these authors visited the same famous birdwatching site Prek Toal in the Sangkae River lowermost reaches (13.24 N, 103.66 E), accessible by boats. Benstead (2006) twice visited this site in early low water season (16.03.2005 and 17.03. 2006) to find "up small forested creeks in the flooded forest" two species, *Agriocnemis pygmaea* and *Acisoma panorpoides* (for



the authorities of all species mentioned in the text see Table 1). On 27.06.2003 (late low water season), Jérôme Constant and Koen Smets collected there 11 other species *Agriocnemis minima, Ceriagrion auranticum, Ischnura senegalensis, Sinictinogomphus clavatus, Brachythemis contaminata, Crocothemis servilia, Neurothemis tullia, Pantala flavescens, Rhyothemis phyllis, R. variegata* and *Urothemis signata* (Seehausen et al. 2016). On 16.02.2010 (also early low water season) Roland & Roland (2010) visited the same site to find two species (one added), *B. contaminata* and *Diplacodes trivialis*. On 16.22.2010 (high water season) the Roland famliy revisited it as more focused on Odonata (Roland et al. 2011) and found seven species (adding four): *A. minima, Pseudagrion rubriceps, Ictinogomphus decoratus, Acisoma panorpoides, B. contaminata, Tholymis tillarga* and *Trithemis pallidinervis*. So, 18 species of Odonata have been reported for Lake Tonle Sap before my visits, and only for one place. The report of *S. clavatus* by (Seehausen et al. 2016) was the first and remains the only for Cambodia.

Hence, Cambodia appeared to harbour a gem of a huge and peculiar wetland as yet largely unexplored with respect to Odonata, which could not be missed in my odonatological studies of Cambodia. My expectation ranged from a handful of widespread 'boring' lentic species to something fitting the lake's uniquity. I examined the lake's

northern bank four times, in the beginning of the low water season (ca 20% of the maximum level) in February/March 2017, at the end of the low water season (10% of the maximum level) in June 2018, at the end of the high water season in November 2018 (ca 80% of the maximum level, ca 01.5 m below it) and a rather intermediate but already decreased level (ca 30%) in December 2019. On these four visits, 12 full days were in total devoted to the lake and its immediate surroundings (Fig. 13). The results were somewhat intermediate to the two expectation options: a handful of widespread lentic species plus something unexpectable: a new subspecies of *Macrogomphus phalantus* Lieftinck, the species previously thought to occur in swamped forests of Borneo and Sumatra and to be very rare (Kosterin 2019a). These results are outlined below, in spite of inevitable difficulties of describing dragonfly communities of fluctuating habitats. Because of this, below I first make an attempt to do this in a locality-wise order, and provide a checklist of species found with reference to localities at the end of the paper. I include only the data from seasonably flooded areas near the lake (Fig. 13) and

Figure 5. Fish traps at banks of Lake Tonle-Sap at the low water season at its different levels and state of the water. Photos by Eddie Smith.

Figure 6. Cham fishermen floating villages in Lake TonleSap.

do not mention those from firm lands around, like the Angkorian temple area, which will be considered elsewhere.

These studies were greatly facilitated by Eddie Smith, a microlight pilot from Siem Reap, who has been flying above the region for already 17 years and who shared a great amount of useful information about it, offered an aerial overview of the study area and generously granted a permission to use his aerial photos to illustrate this paper (his photos are indicated in captions, others are by the author).

Methods

The lake periphery was accessed by a small motorcycle Honda Dream C125 or 'tuk-tuk' (a wagon driven by a motorcycle of the same type) via roads, sometimes going along embankments surrounded by water. In the high water season, the stilted villages were accessed by big motor boats (Fig. 14, above) while the inundated forest was accessed by flat-bottomed rowing boats driven by local boatmen or boatswomen (Fig. 14, below), also used in Preak Toal village environs in intermediate season. Common species were recorded by sight, some specimens were collected and stored in

the author's collection and in the Naturalis Biodiversity Center, Leiden, the Netherlands. Photographs of landscapes and Odonata (in purely natural conditions, never posed) were taken with Olympus Camedia C8080 or Canon EOS 350D cameras with a Sigma AF 24-70 mm F2.8 EX DG MACRO lens. Coordinates are provided in the decimal degree format. They were recorded by Garmin eTrex H personal GPS navigator but the provided ranges for the areas actually examined were revised using Google Earth. The elevations are not provided since all they were several metres above sea level while neither the GPS navigator nor Google Earth are precise enough to provide correct fine values. The dates are provided in the dd.mm.year format. The photographs of odonate made during this study have been submitted to iNaturalist.com (see the user @oleg_kosterin and the project 'Odonata of Cambodia'). The material is delivered according to the following principles (if appliable): (i) localities from east to west (but

Figure 7. Cham fishermen floating villages in Lake Tonle-Sap. Photos by Eddie Smith.

with the westernmost Phnom Penh, which is not actually at the lake, added at the end); (ii) sublocalities from the lake bank towards inland; (iii) dates from the late high water season (November) to the late dry season (June) and then to intermediate season (December).

Localities

Kampong Khleang (KK)

Kampong Khleang is a big stilted fishing village (Fig. 15) with some 30 thousand inhabitants (Kampong Khleang Commune, Soutr Nikom District, Siem Reap Province) situated at the lake NEE bank at the mouth of the former ancient canal going from the Phnom Kulen Mts to the lake, once used for irrigation and rock transportation. Presently the canal exists only downstream the village and only its former walls are still noticeable upstream. An area downstream the village is occupied by seasonably flooded forest (Figs 16-17). The canal further enters a 23 km long lagoon (seen in Fig. 13) separated from the main lake by a forested spit. Examined only on 07.11.2018 in the late high water season. In sum 11 odonate species registered.

KK1. (9 species) The inundated forest near the lake-faced village margin (Figs 16-17). 13.093-095 N, 104.111-120 E. The trunks of rather low trees were deeply inundated up to their crowns, which were densely braided with the winding Ivy Woodrose (*Merremia hederacea* (Burm. f.) Halier f.; Concolvulaceae) with small yellow flowers. Actually this represented the most widespread type of the seasonably flooded forest at Lake Tonle Sap.

Figure 8. Asian openbill storks at Lake Tonle-Sap. Photos by Eddie Smith.

Figure 9. The Sangkae River/Lake Tonle Sap joint floodplain as seen from the plane Siem-Reap – Bangkok on 15.12.2019, with many small roundish reserves and the road from Mukh Paen village seen. Collection points MP1, MP2 and MP3 are indicated (see the text).

Broken ends of lower branches in shade were mostly covered with some grey sponges but no bivalve colonies were seen. Open areas of water were mostly covered with large matts of *Persicaria* sp. (with long stolones and erect, narrow white inflorescences), interspersed with water hyacinth and water cabbage (Fig. 18). At these matts, *Pseudagrion microcephalum* and *P. rubriceps* occurred at similar low numbers (one male of each collected); among them one female of *Agriocnemis nana* was collected. Dragonflies were represented by *B. contaminata* and *O. sabina* (frequent at any vegetation type but not numerous); one male *U. signata* and *T. pallidinervis* perched on tall dry branches of *Mimosa pigra*, and 2-3 individuals of *R. phyllis* fluttering over the water. Quite often *T. tillarga* were seen in their characteristic, swift and erratic flight in deep shaded gaps between inundated trees.

KK2. (6 species) A road embankment by the canal inside the village, at the pagoda. 13.125-126 N, 104.121-122 E. Houses and shrubs on the embankment; the water almost entirely covered with water hyacinth leaving scarce openings, some patches of *Persicaria* sp. and Elephant Eear (*Colocasia* sp. or *Alocasia* sp.), inundated shrubs (mostly *M. pigra*) and solitary low trees (Fig. 19). Numerous *B. contaminata*, quite a few *C. servilia*, again one perching male of each *U. signata* and *T. pallidinervis*, one flying *P. flavescens*.

Kampong Pluk (KP)

Kampong Pluk (or Kampong Phluk) is a stilted village (Figs 20-22) of about 3 thousand people (Kampong Phluk Commune, Prasat Bakong District, Siem Reap Province) which is the closest to the city of Siem Reap and most popular among tourists, as a curious settlement and because of retaining nearby the largest area of seasonably flooded forest. Alike Kampong Khlaeng, Kampong Pluk is situated near the mouth of the ancient, ca 36 km long and a thousand years old, Roluos Canal starting at the Phnom Kulen Plateau in the north-east. Unlike the canal at Kampong Khlaeng, Roluos Canal exists until present (Figs 23). It enters Lake Tonle Sap immediately, without any lagoon. In 14.5 km N of Kampong Pluk, Roluos village is situated, with Bakong, Lolei and Preah Ko Temples, where Hariharalaya, the first capitol of the Angkor Empire, was established by its founder Jayavarman II around the first years of IX century. The area was examined in the early low level season, late low level season and late high level season. In sum 28 species registered.

Figure 10. Carpets of water hyacinth: above - fresh in a swamp 2 km NE of Phnom Krom Hill (locality PK1, see below, 3.11.2018 and 12.12.2019): below - dry in a temporary fishing village between Phnom Krom and Kampong Pluk (locality WF2, see below, 13.06.2018).

KP1. (15 species) The seasonably flooded forest between the village and the mouth of the Roluos Canal. 13.195-204 N, 103.971-975 E. The forested area starts at the village, continues for 1 km at both sides of the canal to its mouth, has a rhomboid shape and is 650 m in its broadest place but then again extends along the very lake bank. It was studied only at the western side of the canal. At its SW side the forest was obviously replanted since young trees are disposed in rows, elsewhere it looks pretty natural, and very weird because of rather tall and very thick trees with twisted trunks and branches. I did not observe this forest type elsewhere (although there may be further areas of similar forest to the east of the village, as may be judged from the air). At the forest margin facing the lake open bank as well as its western margin, lower trees appear similar to those at Kampong Khlaeng. Further to the west they are replaced by scrub (with a big share of *M. pigra*) thickly covered by ivy woodrose.

At the high water season the trees were inundated up to the branching crowns (Fig 24a-b). A family of crab-eating maca-

Figure 11. Vegetation at the Sangkae River mouth (close to Loc. PT) is formed by three alien species of different origin: Arundo donax **(cane)**, Mimosa pigra **(scrub) and** Eichhornia crassipes **(floating). 10.12.2019.**

ques (*Macaca fascicularis* Raffles, 1821) wandered near the village over the tree crowns and a pavement made through (Fig. 25), waiting for boated tourists to feed them. The water was slightly greenish turbid. The floating vegetation was represented

Figure 12. Dead colonies of small mussels on branches of trees of temporarily inundated forest at the northern bank of Lake Tonle Sap, at its low level season, at Kampong Pluk village (24.02.2017, above, and 15.06.2018, below).

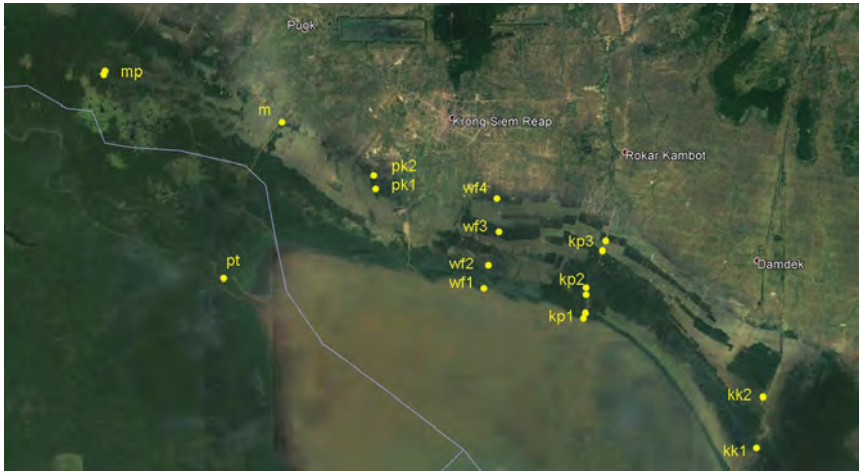


Figure 13. Disposition of sited examined at Lake Tonle-Sap in 2017-2019 shown on a Google Earth cosmic image. For explanations see the text.

Figure 14. Big boats bound to Kampong Pluk village at the high water season (2.11.2018) (top) and a small flat-bottomed boat used for examining of the Prek Toal area (10.12.2019) (bottom).

exclusively by water hyacinth forming small patches under the forest and at the lake very bank and large matts at open places among trees. Odonates were searched for on 02.11. 2018, at 9:40-12:00 a.m.; 11 species were found. In the shade of the forest canopy they were represented by rather abundant *B. contaminata* (near water hyacinth patches and emerging branches), not infrequent *O. sabina* (at branches) and *P. rubriceps*, few *P. microcephalum* and one female (collected) of *Ceriagrion praetermissum* (the damselflies kept to water

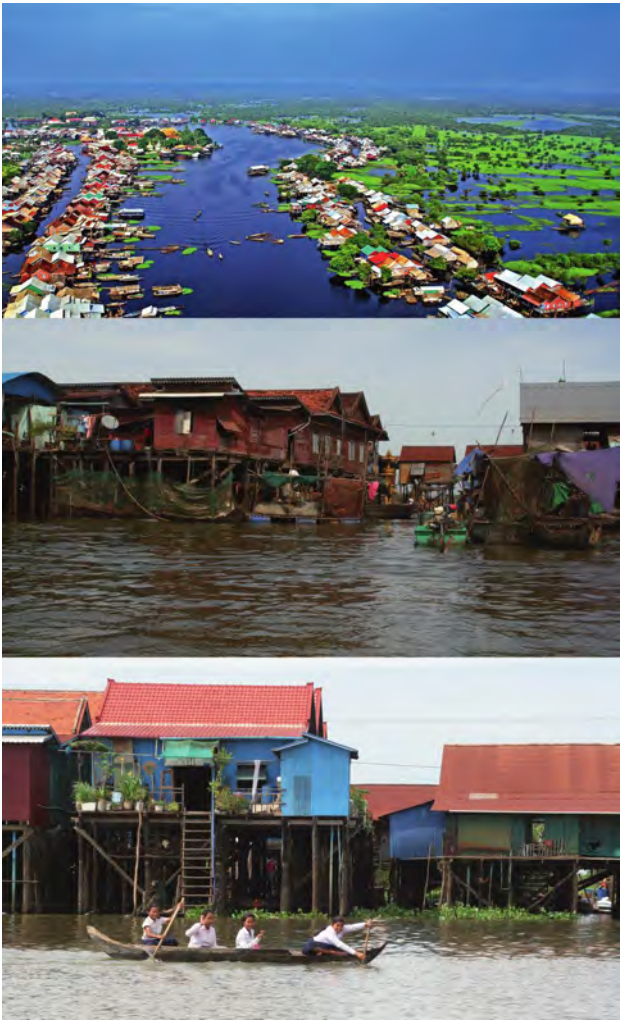


Figure 15. The stilted village of Kampong Khlaeng. Top photo by Eddie Smith, middle and bottom photos by the author.

hyacinth). A male of *T. tillarga* (collected) was startled from a tree branch. At sunny areas of open water at the western margin of the forest (Fig. 26), odonates were more abundant. *O. sabina* and *P. rubriceps* remained most numerous and *P. microcephalum* were quite frequent but *B. contaminata* became few. There were several females of *C. servilia* and one bright male of *U. signata* (at a water hyacinth patch). At larger open water areas several *T. pallidinervis* perched on tall stems of *M. pigra* (both sexes photographed, Fig. 27). Above open water areas at the tall forest margins, quite a few *R. variegata* and less frequent *R. phyllis* fluttered and quite many *T. tillarga* were flying (in spite of the sun) along trees at a considerable height.

Figure 16. Lower inundated forest at Kampong Khlaeng village (loc. KK1) at the high water season (7.11.2018).

Figure 17. Taller inundated forest at Kampong Khlaeng village (loc. KK1) at the high water season (7.11.2018).

When examined at the early low water season (24.02.2017, at 12 a.m. – 2 p.m.), there was no water in the forest, a bush understory was released from water but the ground was muddy and sticky and had scarce grass (Fig. 28). Odonates were almost absent from the forest: I only managed to startle two females of

Figure 18. Floating patches of Persicaria **sp.,** Pistia stratiotes **and** Eichhornia crassipes, **Taller inundated forest at Kampong Khlaeng village (loc. KK1) at the high water season (7.11.2018).**

Figure 19. Inundated open scrub (mostly Mimosa pigra**) and open tree stand at the canal in Kampong Khlaeng village near the pagoda (loc. KK2) (7.11.2018).**

T. tillarga and to find two males of *P. rubriceps* at bushes by the canal bank (1 photographed). Closer to the lake the mud became deep and sucking and reached a knee depth, then muddy green water appeared and became deeper so that a knee deep mud was gradually replaced with a knee deep water at the forest margin facing the lake open surface, which actually marked the lake bank (Fig. 29 below). The tree branches were speckled with dead colonies of small mussels. Along the bank. *B. contaminata* was extremely abundant, among which *O. sabina* were frequent. The shrubs at the western forest margins (Fig. 30) were covered with thick layers of dry water hyacinth and alive and dead ivy woodrose which formed mounds upon which I could climb. Numerous *T. tillarga* were startled from these bushes and started to fly along them, sometimes by several at once, but seemed to be all females (at least I did not see a single red mature male) There were quite many flying *R. phyllis* and *R. variegata*,

Figure 20. The stilted village of Kampong Pluk at the early low water season (24.02.2017).

Figure 21. The stilted village of Kampong Pluk at the high water season. Photos by Eddie Smith.

Figure 22. The stilted village of Kampong Pluk at the high water season (02.11. 2018).

Figure 23. The Roluos Canal at Kampong Pluk village at the high (left; photo by Eddie Smith) and low (right, photo by the author) water seasons.

which at ca 2 p.m. formed a big swarm on an opening among low trees. Above them, at the height of 3-9 m, about a dozen of *Epophthalmia* ranged, obviously in trophic flight (a later finding and general occurrence in the area suggested these were *E. frontalis*).

At the end of the low water season (15.06.2018, at 8:45 a.m. – 2 p.m.) the ground in the seasonably flooded forest (Fig. 31) was dry and firm but the bank and the closest to it part of the scrub at the western forest margin were just starting to be inundated with a very shallow and quite clear, only slightly turbid water (the bottom was still firm). There were many dragonflies but strikingly not a single damselfly. The dragonflies were mostly associated with the bank of the canal, which still had a turbid reddish water, perhaps because of too heavy motor boat traffic (Fig. 32). There were very many *B. contaminata* (especially at and near water), several ranging territorial males of *E. frontalis* (1 collected), 1 territorial male of *Ictinogomphus decoratus melaenops* (photographed), 2 individuals of *O. sabina* and, surprisingly for such an eutrophic water body, at least 3 males (flying above the water, rarely perching on prominent stems; 1 collected) and a female (ovipositing around a stick shortly protruding from the water 1 m off the bank) of *Pseudothemis jorina*. Under the forest canopy, resting but cautious *T. tillarga* (including mature males, one photographed – Fig. 33) became more frequent closer to the lake.

The waterfront was rimmed with a 20-30 m broad stripe of tall annual bulrush *Actinoscirpus grossus* (L.f.) Goetgh. & D.A. Simpson, which quickly rises around the lake at the end of the dry season (Fig. 29 above). At the time of examination it was already

Figure 24a-b. The forest near Kampong Pluk village (Loc. KP1) inundated by the high Tonle Sap water (02.11.2018).

inundated by shallow rising water. *B. contaminata* expectedly occurred there in great numbers but others were scarce: I met two *O. sabina* (Fig. 34) and one *R. phyllis* and, quite unexpectedly, a not yet fully mature, still yellow-and-black male of *Aethriamanta aethra*, which showed high fidelity to its perch of a protruding branch (Fig. 35a).

Behind (at the NNW margin of) the forest strip going along the lake bank from the canal mouth, there was a kind of a broad 'meadow' with bushes and low trees, being inundated by very shallow water advancing as I watched (this area was studied at 13.195-204 N, 103.971-975 E, some 70-90 m off the lake bank). There were less *B. contaminata*, few *R. phyllis* et *variegata* and two old females of *C. servilia* (Fig. 36c). But above these, there was an incredible surprise: quite a number of big and impressive *Macrogomphus phalantus jayavarman* (males and a posttteneral female) (Fig. 37), some

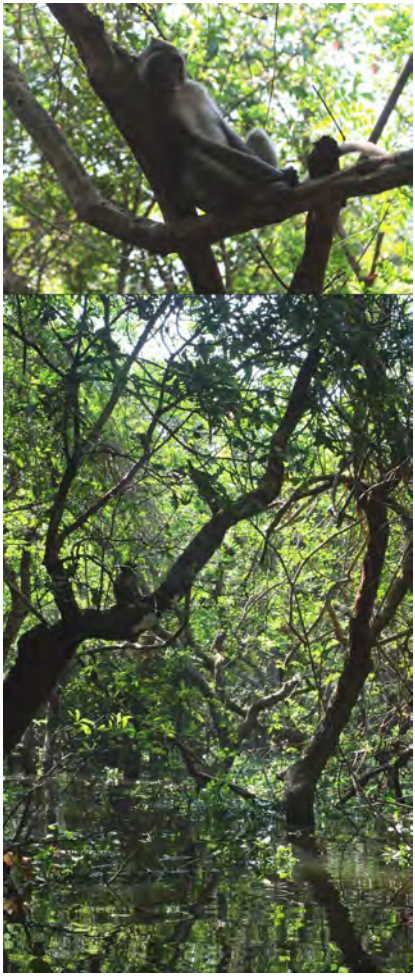


Figure 25. Crab-eating macaques in the inundated forest near Kampong Pluk village (02.11.2018).

Figure 26. Open areas with sparse inundated trees between Kampong Pluk village and Lake Tonle Sap bank (Loc. KP1) at the high water season (02.11.2018).

of which comprised the type series of this taxon (Kosterin 2019a). They sat on vertically hanging tree branches and herbaceous lianas (once two sat on one stem), rarely on prostrate branches, mostly in shade but sometimes under direct sun. Some of them

Figure 27. A male (left) and female (right) of Trithemis pallidinervis **in open areas in inundated forest between Kampong Pluk village and Lake Tonle Sap bank (Loc. KP1) at the high water season (02.11.2018).**

Figure 28. The seasonably flooded forest near Kampong Pluk village (Loc. KP1) in the early low water season (24.02.2017).

Figure 29. The Lake Tonle Sap N bank 1 km S of the margin of Kampong Pluk village (Loc. KP1): below – still inundated in the early low water season (24.02.2017); above – overgrown with annual Actinoscirpus grossus **and started to be inundated again in the late low water season (15.06.2018).**

Figure 30. Scrub covered with ivy wood-rose at the western forest margin near Kampong Pluk village (Loc. KP1) in the early low water season (24.02.2017).

were found deeper in the forest. They were not very cautious: when startled, they flew for some dozen of metres and sat again. Curiously, not a single one was seen at the canal banks. Most probably, these big dragonflies emerged immediately from the lake, although I did not see any exuviae.

KP2. (17 species) The village environs; examined at its western margin at the pagoda, 13.2090 N, 103.973 E, 01.5 km NNE of the lake bank, and its northern end, 13.220 N, 103.974 E, 2.8 km from the lake. There was patchy scrub,

Figure 31. The seasonably flooded forest near Kampong Pluk village (Loc. KP1) in the late low water season (15.06.2018).

Figure 32. The lowermost reaches of the Roluos Canal crossing the seasonably flooded forest in southern vicinities of Kampong Pluk village (Loc. KP1) in the late low water season (15.06.2018), at that time inhabited by Ictinogomphus decoratus, Epophthalmia frontalis **and** Pseudothemis jorina**.**

at the pagoda also open tree stand (Fig. 38), both trees and bushes being thickly covered with ivy woodrose, and scarce giant cane. This area was examined only in the low season, since in the high season it is inundated by deep water. In the early low season (24.02.2017, at 11:30-12 a.m. and at 3-3:30 p.m. at the pagoda) the trees and bushes were still green while the ivy woodrose covering them partly green and partly

Figure 33. A male of Tholymis tillarga **in shade of the seasonably flooded forest at Kampong Pluk village (Loc. KP1) in the late low water season, 15.06.2018.**

Figure 34. A male of Orthetrum sabina **eating a male of** Brachythemis contaminata **on a dead, dry colony of small mussels at the N bank of Lake Tonle Sap 1 km S from the margin of Kampong Pluk village (Loc. KP1) in the late low water season, 15.06.2018.**

Figure 35. A not fully mature male (a), mature male (c) and a female (b) of Aethriamanta aethra **in the late low water season: a - at the N bank of Lake Tonle Sap 1 km S from the margin of Kampong Pluk village (Loc. KP1), 15.06.2018; b and c – at a big lotus swamp 3 km NW of the Phnom Krom hill (Loc. PK1), 18.06.2018 .**

dry. Among trees and bushes, various pools with yellow water remained, and also bigger ponds near the pagoda. All they were partly covered with floating patches of water hyacinth, fresh-green with some flowers. Unlike in the inundated forest at that time, damselflies were not infrequent there, as represented by *I. senegalensis* and *Agriocnemis*, a number of which I checked in hand and found only *A. minima* at the pagoda and *A. pygmaea* at the village northern end. Dragonflies were representing by fluttering *R. phyllis* (Fig. 39) and *R. variegata* (quite frequent), soaring *P. flavescens* (few), perching on tall sticks *I. decoratus* (3 ♂♂ seen, 1 photographed – Fig. 39) and *U. signata* (quite many ♂♂, 1 collected, 1 photographed – Fig. 40a), and keeping to vegetation *Rhodothemis rufa* (several ♂♂ seen, 1 photographed – Fig. 41a, 1 ovipositing ♀ collected, 1 more ♀ photographed – Fig. 42a), *C. servilia* (several, 2 ♂♂ photographed sitting side-by-side - Fig. 36a), *B. chalybea* (1 ♂ photographed), *N. tullia* (several, 1 ♂ photographed – Fig. 43), *O. sabina* (several), while *B. contaminata* (many) kept to the water, *A. panorpoides* (1 ♂ seen) to water hyacinth and *D. trivialis* (1 ♂) to the ground. A short stop in the late low season (not taken into account in Table 1) on 15.06.2018 revealed only quite many *B. contaminata* and a male of *I. decoratus*.

Figure 36. Males (a-b) and a female (c) of Crocothemis servilia**: c - near the Lake Tonle Sap bank 1 km S from the margin of Kampong Pluk village (Loc. KP1) 15.06.2018.**

KP3. (20 species) The flatland NNE of Kampong Pluk. Similar places separated from each other for 3 km were studied in the late low level season in February 2017 and in the high level season in November 2018, since in the second case the former place was inundated and no boat was available in that area. In June 2018 the elevated road to the village was being reconstructed that made the area inconvenient for study.

The area studied in the high level season on 2.11.2018 (1:50-3:10 p.m.) was in the coordinate range of 13.273-275 N, 103.987-992 E and 8.7 km NE from the lake bank. There was a low embankment separating two big areas quite deeply inundated by the lake water, a rice field on its SSW side (loocking as a vast open water surface with nothing emerging) and scrub on its NNE side. Evidently the embankment had not long ago appeared from water and was not yet completely dry; a trace on a pole evidenced that the maximum water level was some 1.5 m above it. The water between bushes of scrub was almost completely covered with water hyacinth and also some patches of thin Poaceae grass (Fig. 44). The scrub abounded in pond herons (*Ardeola speciosa* Horsfield, 1821 or *A. bacchus* (Bonaparte, 1855)). I examined few places where it was possible to descend from the embankment to the water and at one of them, among water hyacinth I found several *A. minima* and two bright red males of *C. praetermissum* (collected). Net sweeping on the scarce grass at the embankment sides provided a male of *I. senegalensis* and numerous *D. nebulosa*,

Figure 37. A male of Microgomphus phalantus jayavarman **in its type locality, at the margin of open and low seasonably flooded forest margin Lake Tonle Sap bank 1 km SSW of the margin of Kampong Pluk village (Loc. KP1) 15.06.2018.**

Figure 38. Pools in open tree stand at the western margin of Kampong Pluk village near the pagoda (Loc. KP2) in the early low water season (24.02.2017).

which was the most frequent dragonfly. Other dragonflies were also abundant and diverse: there were also numerous (mostly males) *C. servilia*, *T. pallidinervis*, *O. sabina* and *N. tullia* and fewer but still many *B. contaminata*, quite a few *R. variegata* and *R. phyllis*

Figure 39. A male of Ictinogomphus decoratus melaenops **eating** Rhyothemis phyllis **at the western margin of Kampong Pluk village near the pagoda (Loc. KP2), 24.02.2017.**

Figure 40. Males of Urothemis signata**: a - at the western margin of Kampong Pluk village (Loc. KP2), 24.02.2017**; **b - 3 km NE of the Phnom Krom hill (Loc. PK1), 26.02.2017.**

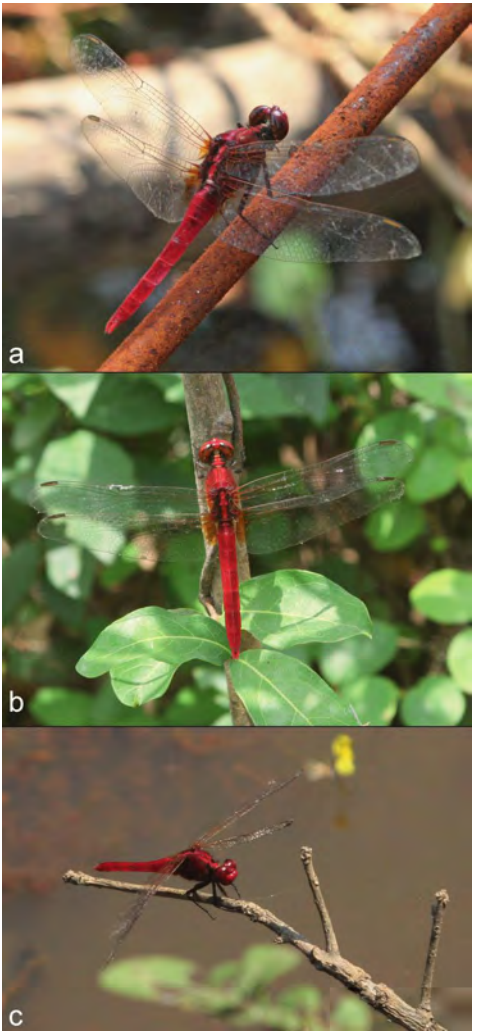


Figure 41. Males of Rhodothemis rufa**: a - at the western margin of Kampong Pluk village (Loc. KP2), 24.02.2017**; **b - 3 km NE of the Phnom Krom hill (Loc. PK1), 18.06.2018**; **c – at a scrub margin 10.7 km SSE of Siem Reap (Loc. WF3), 01.03.2017.**

in the air and *A. panorpoides* on water hyacinth. Infrequent were *T. tillarga* (2 already active ♂♂ seen), *Brachydiplax sobrina* (1 ♀ photographed – Fig. 45), *B. chalybea* (1 ♂ seen), *P. flavescens* (one soaring) and *R. rufa* (1 ♀ seen).

The area studied in the early low level season on 24.02.2017 was in the coordinate range of 13.251-253 N, 103.985-988 E and 6 km NNE from the closest lake bank. This was at the opposite, southern side of the above mentioned big rice field, just southerly of its margin and the beginning of the scrub area which extends to the lake not interrupted by any more fields. And it was a fairly weird terrain looking gloomy and absolutely dead, unlike anything I have seen on the earth (Fig. 46). The ground was almost barren, with very scarce grass and some rosette annual plants; sparse and dead-looking bushes and low trees stood above it. They were completely dry and thickly covered with thick carpets of dry ivy woodrose which incorporated quite a lot of dead water hyacinth and sheets of dead thread algae. (Actually on the same day immediately at Kampong Pluk (KK1) I saw the same vegetation but green and full of life, with the ivy woodrose blooming.) There were scarce very shallow and muddy pools with yellow water and several flowering groups of water hyacinth. There were scarce *I. senegalensis*, *A. pygmaea* and *B. contaminata*. Near the embankment, a deep ditch went across the terrain with slightly turbid running water, most probably pumped from somewhere upstreams. There were numerous *B. contaminata*, quite many *I. senegalensis* (including tandems, photographed), few *A. pygmaea* and not less than 3 ♂♂ (1 collected) and 1 ♀ (collected) of *P. rubriceps*. On a very short but partly green grass nearby, *D. trivialis* were frequent (mostly immature, greenish, but mature

Figure 42. Females of Rhodothemis rufa**: a - at the western margin of Kampong Pluk village (Loc. KP2), 24.02.2017**; **b - 3 km NE of the Phnom Krom hill (Loc. PK1), 18.06.2018.**

Figure 43. A male of Neurothemis tullia **at a small pool at the western margin of Kampong Pluk village near the pagoda (Loc. KP2), 24.02. 2017.**

Figure 44. Inundated scrub with water hyacinth behind an embankment 8.7 km NE of Kampong Pluk village (Loc. KP3) at the high water season, 02.11.2018.

bluish males also occurred) and several *Ischnura aurora* were rather unexpectedly found (3 ♂♂, 1 ♀ collected 1 ♂ photographed – Fig. 47). The latter were so tiny and had curious shaking flight that were overlooked by me and discovered only by my 6 years old son Valentin (Fig. 46 below). There were also a shallow ditch along the high embankment of the main road, with a tiny stream seeping over red mud. There were again numerous *B. contaminata* and quite many *O. sabina*, while net sweeping over low fine grass provided many *Argyocnemis*, of which I collected 4 ♂♂ and 2 ♀♀ of *A. pygmaea* and 2 ♂♂ 1 ♀ of *A. minima*.

Road to the watermelon field (WF)

I studied the area on the way from the eastern Siem Reap suburbs at ca 13.31 N, 103.90 E to WSW, towards an illegal watermelon field near the lake very bank at 13.22 N, 103.89 E, which is completely inundated at the high lake level. Most of this road serves as the border of Chreav District (Sangkat) of Siem Reap Municipality

Figure 45. A female of Brachydiplax sobrina **at inundated scrub 8.7 km NE of Kampong Pluk village (Loc. KP3), 02.11. 2018.**

(Krong Siem Reap) to the west and Prasat Bakong District of Siem Reap Province to the east, but close to the lake bank it enters the Sangkat Chreav territory.

Several parallel elevated roads go from populated area to the south through an 1 km broad belt of seasonably flooded scrub and join a perpendicular high latitudinal embankment at right angles at ca 13.29 N, with a road between two rows of tall eucalypts, which serves as a dam holding water in the scrub northerly of it to feed vast rice fields to the south. A lake-bound road at ca 109.90 E crosses the embankment, passes 2 km through the rice field and enters a next scrub zone, again 1 km wide, then for some 800 m follows a next contiguous stripe of rice fields and then alternating patches of inundated forest, bushes and rice fields. Before the end of the road, at the last rice fields, in the low season there is a very small temporary fishing village, then a stripe of seasonably flooded tall bushes/low trees 1 km wide, inside which, very close to the Lake Tonle Sap bank, there is a cleared area of an illegal watermelon field some 700 m long (13.224-229 N, 103.885- 890 E), which served as a landmark. At the high level season all this area is inundated, most probably except for the high eucalypt road.

In sum 30 species registered.

WF1. (9 species) The Tonle-Sap bank (13.2217-2227 N, 103.8870 E; 15.7 km SSE from the Siem Reap Centre; Sangkat Chreav territory. Accessible in the late low level season, studied on 13.06.2018 at 1:10-2:30 p.m. At the moment of examination, the water edge reached last trees (with dead bivalve colonies on branches up to 3 m above the ground!), then there was a very broad (ca 100 m wide) stripe of bulrush (*A. grossus*) emerging from water, which at its lake-facing margin reached the depth just above knee. The bulrush was sparse at the bank but became thick as the water deepened

Figure 46. Dry scrub 6 km NE of Kampong Pluk village (Loc. KP3) at the eraly low water season, 24.02. 2017.

(Fig. 48). The bottom was slightly sticky, the water was slightly turbid, reddish; almost hot in its shallowest parts and becoming moderately warm to the inner margin of the bulrush stripe where it got a smell of animal rot (dead snails?); open surface clean and wavy. There were an immense number of both sexes of *B. contaminata* (1 ♂ photographed), a school of which followed me in their accompanying behaviour. Closer to the bushes *C. servilia* were frequent (yellow individuals being more frequent than red males) and I repeatedly startled *I. decoratus*. Other odonates were very scarce. Two males (collected, 1 photographed – Fig. 49a) of *P. microcephalum* were found above the shallowest water, and one individual of each *R. phyllis* and *R. variegata* fluttered over this zone. In thick bulrush I found only a male of *P. rubriceps*, a copula of *I. senegalensis* (photographed) and a male of *B. chaybea*. No *O. sabina*! It seems that the shallow water of the bulrush zone was very low of oxygen so that even the commonest lotic species were depleted, but this obviously did not concern *B. contaminata*.

WF2. (16 species) From the temporary fishing village to the watermelon field, 13.226-247 N, 103.889-892 E; 13-15 km SSE from the Siem Reap Centre, 0.2-2.7 km from the lake bank; Sangkat Chreav District territory. Not acces-

Figure 47. Males of Ischnura aurora**: a - at a ditch in dry scrub 6 km NE of Kampong Pluk village (Loc. KP3) 24.02.2017**; **b - at the Mekong right bank in the Phnom Penh Centre (Loc. PP), 28.02.2017.**

Figure 48. The Lake Tonle Sap N bank 15.7 km SSE of Siem Reap (Loc. WF1) at the lake low water season (13.06.2018), with a broad bulrush (Actinoscirpus grossus**) stripe in water and low seasonably flooded forest on the bank (seen from distance on the lower photo).**

sible in the high water season; examined on 01.03. 2017 (Fig. 50), 13.06.2018 (Fig. 51) and 12.12.2019 (Fig. 52).

The lake bank is separated from the fishing village by thickets of tall bushes and low trees (of course all braided by ivy woodrose), through which a very bad tractor ground road goes for 700 m (13.226-233 N, 103.889-190) to the watermelon field; it was always badly trampled by buffalos and in December very muddy (Fig. 52 below). I shortly examined it on all the three above mentioned dates and in two cases found no dragonflies. On 01.03.2017 (1:50-2:30 a.m.; early

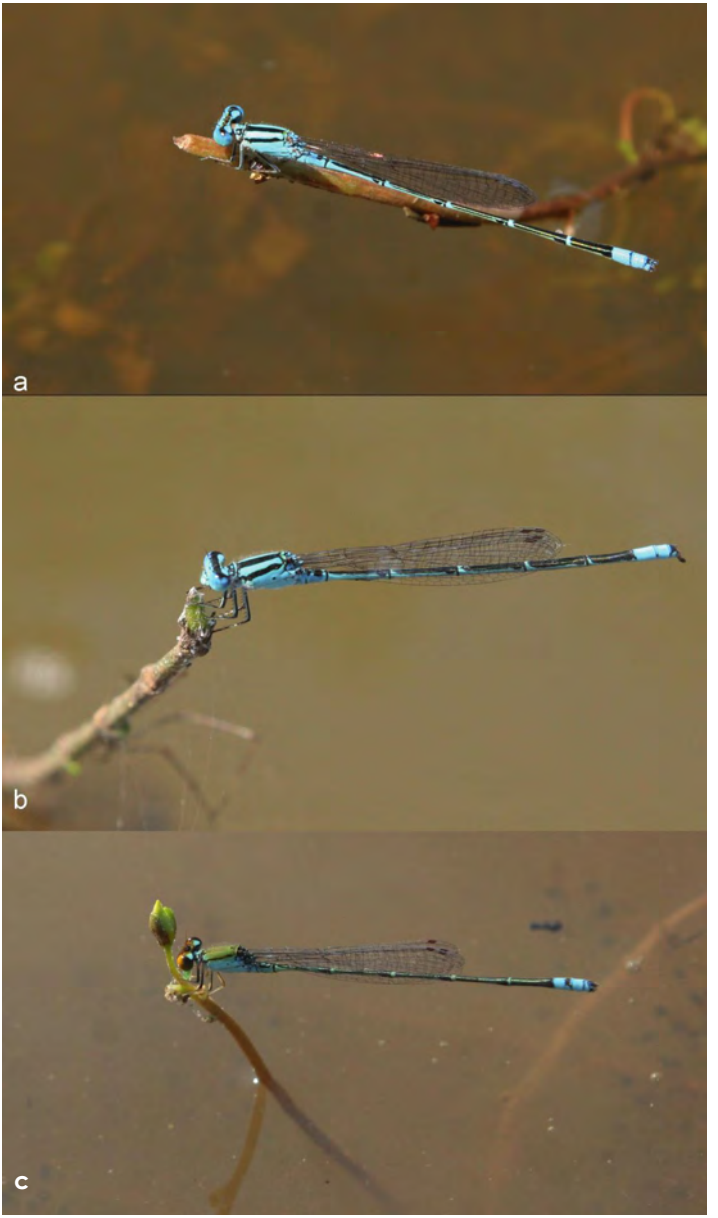


Figure 49. Males of Pseudagrion **spp. perching at open water: a – P. microcephalum among shallowly inundated bulrush at the Lake Tonle Sap N bank 15.7 km SSE of Siem Reap (Loc. WF1) 13.06.2018; b –** P. australasiae **in inundated scrub 9 km SE of Siem Reap (Loc. WF4), 05.11.2018; c –** P. rubriceps **in shallowly inundated scrub 4.5 km NNW of the Phnom Krom hill (Loc, PK2), 05.11.2018.**

low season) I was surprised to encounter there nine individuals of *Aethriamanta* sp. perching on tips of thin dry branches at the height of 2-3 m above the ground. Of them I managed to collect 7, 6 of which appeared to be females, 3 of *A. aethra* and

Figure 50. Swamps and rice fields divided by an embankment with a temporary fishermen tent village 13-15 km SSE of Siem Reap (Loc. WF2) at the early low water season (01.03.2017).

2 of *A. brevipennis*, the remaining one was a young male of *A. aethra*. No doubt they bred from the nearby deep and hardly accessible swamps covered with water hyacinth, where mature males (which I did not see) should have awaited the females feeding at the margins of the surrounding thickets which I by chance found concentrated at that road.

The temporary fishing village (13.233-246 N 103.890-892 E) was composed of canopies on poles at both sides of the embankment with a 01.5 km long road from NNE to SSW, not better than described above, to the west of which there was a big rice field (Figs 50, 52) and to the east quite deep swamps full of water hyacinth and with sparse quite tall trees (Figs 50-52). On 01.03.2018 the rice was young and green (Fig. 50), on 13.06.2018 the fields were dry and on 12.12.2019 still partly inundated (Fig. 52). On 01.03.2018 the swamps were still waist deep (Fig. 50) and *Pistia stratiotes* and *Salvinia cucullata* Roxb. ex Bory were seen in water hyacinth. On 13.06.2018 the swamps were shallow and some areas were dried to deep mud covered with a thick carpet of water hyacinth (Fig. 10 below); the water became yellowish and some microscopic algae developed on the surface (Fig. 51); *Salvinia* became more abundant while *Pistia* was not noticed, and big patches of bulrush appeared. On 12.12.2019 the swamps were deeply inundated (Fig. 52) so that many boats were parked at the village. *B. contaminata* was invariably very numerous at

Figure 51. Deep roadside pools with water hyacinth at Loc. WF2 at the late low water season (13.06.2018).

the embankment and swamp margins at any season and at any visit; *C. servilia* was numerous and *O. sabina* frequent on 01.03.2018 and 12.12.2019 but on 13.06,2018 (late low season) only one male of each was met. On 01.03.2018, several *D. trivialis* (including mature males) and males of *U. signata* were seen and on 12.12.2019 many *T. pallidinervis* and one *R. variegata*. On 01.02.2018 many *A. pygmaea* (4 ♂♂ checked in hand) and 1 male of *I. senegalensis* were found at the inundated, fresh green rice field.

At the far (lake-side) end of the embankment there were deep roadside pools filled with water hyacinth and scarcely accessible because of the quite steep embankment and thorny bushes of *M. pigra* (Fig. 51). On 12.12.2019 they were still merged to the inundated larger swamps. On 01.03.2018 I found there only a male of *A. panorpoides*. On 13.06.2018 there were remarkably many *Ceriagrion auranticum* (2 ♂♂ collected) and *C. praetermissum* (4 ♂♂ 1 ♀ collected), among which I managed to find a male and an immature (red) female of *A. minima*.

WF3. (13 species) The elevated ground road with accompanying ditches, a small pool and a narrow rice field inside the broad stripe of seasonably flooded scrub (Fig. 53) dammed by the embankment parallel to the lake bank and closest to it. (On 12.12.2019, when the lake was shrunken, I saw how this worked: the water flowed through a pipe in the embankment from the scrub towards the lake, feeding the rice field). 13.2697-2712 N, 103.8977-8984 E, 10.7 km SSE from the Siem Reap centre, 5.2 km NNE from the lake

Figure 52. The same place as in Fig. 49 (Loc. WF2) but at the intermediate water season (12.12.2019).

bank (Sangkat Chreav/Sangkat Prasat Bakong border). Not accessible in the high level season; examined on the same days as WF2. On 01.03.2017 there were quite many *B. contaminata*, many *C. servilia* (mostly females, from yellow young to brown mature ones; 1 ♂ photographed), frequent *R. phyllis* and *variegata*, several *D. trivialis* (on the road), a male (photographed – Fig. 41c), two females of *R. rufa* and one *P. flavescens*. One of the roadside ditches contained quite a deep water without aquatic vegetation but with patches of dense fine semi-inundated grass, the net sweeping of which provided many males of *A. pygmaea* (5 checked in hand), 2 males of *I. senegalensis* and a female of *D. nebulosa*. The opposite ditch had shallow dark pools with flowering *Utricularia* sp., upon which a male of *I. decoratus* perched on a dry bush branch.

On 13.06.2018 (late low season) many *B. contaminata*, few *D. trivialis* and even a male of *I. decoratus* were again observed, but no other dragonflies. Only very shallow pools left in the deeper ditch (Fig. 53, above), over which there was a lonely male of a blue *Pseudagrion* (*P. australasiae* or *P. microcephalum*), which I failed to catch because it was attacked by a male *B. contaminata* (who missed it as well).

On 12.12.2019 I was surprised to find only one male of usually abundant *B. contaminata* but quite many *O. sabina* and *T. pallidinervis*, several (red and yellow) *C. servilia*, and one immature *D. trivialis*.

WF4. (19 species) The most inland broad stripe of seasonably flooded scrub (Fig. 54) dammed by the elevated road with eucalypts which serves as a reservoir for the vast rice field behind the dam, as well as for fishing. At the northern side there is some

Figure 53. A narrow rice field in seasonably flooded scrub 10.7 km SSE of Siem Reap (Loc. WF3): above - at the late low water season (13.06.2018); below – at the intermediate season (12.12.2019).

deeper water reservoir (ca 230 x 200 m) with open water, also used for fishing. At the high level season the water at the embankment (ca 13.291 N) was more than a waist deep, gradually became shallower to the north to disappear at ca 13.30 N. At the late dry season only very shallow pool remained along the dam, which, however, deserved a study. Unfortunately, the area was studied (ca 450 x 300 m; 13.291--295 N, 103.909-911; 9 km SE of the Siem Reap centre) only at the high level season on 05.11.2019 (9:30-11 a.m.) and the late intermediate season (shortly in the evening of 02.12.2019 and at 12 a.m. – 13:15 p.m. on 12.12.2019). Most thoroughly studied was the area of some 150 x 150 m (13.294-295 N, 103,909-910 E) where the water was conveniently about knee-deep and the bushes (including *M. pigra*) were sparser. A remarkable feature of the place was the abundance of flowering floating plants, lilac *Rotala* sp., yellow bladdenwort (*Utricularia* sp., like *U. aurea* Lour. but with curiously thick floats – Fig. 55), white water lily (*Nymphaea* sp.) and water snowflake (*Nymphoides indica* (L.) Kuntze), the latter being especially abundant in December (Fig. 54, except for the top photo). Curiously, there was no water hyacinth there.

Figure 54. Inundated scrub 9 km SE of Siem Reap (Loc. WF4), a habitat of diverse odonate assembly; top photo – at the high water season (05.11.2018); other photos – at the intermediate season (12.12. 2019). The white spots in the lowest and second top photos are the water snowflake (Nymphoides indica**), those in the second low photo are egrets.**

There was also sparse and thin emerging grass, to which in November quite a few damselflies were confined: *Aciagrion borneense* (many ♂♂, seemingly aggregated; 4 collected, some photographed – Fig. 56), *I. senegalensis* (few ♂♂ and ♀♀; 1 ♀ collected), *P. australasiae* (few very actively flying ♂♂, 2 collected, 1 photographed – Fig. 49b), *P. calamorum* (few ♂♂, conspicuous whitish on the broad leaves of *Nymphaea* and *Nymphoides* which they occupied; 2 ♂♂ photographed – Fig. 57b), *A. minima* (1 ♀ photographed), *P. rubriceps* (1 ♂ at a deeper place). In December the environment looked similar (but a mass flowering of water snowflake) but the damselflies were almost absent: for more than an hour I found only a male, a female (collected) and copula of *I. senegalensis* (Fig. 55) and, at the smaller water reservoir, a male of *A. pygmaea* (collected).

The dragonflies were diverse in November: *O. sabina* (very many everywhere), *C. servilia* (many, both sexes), *T. tillarga* (many active between bushes in the morning), *T. pallidinervis* (many ♂♂ on sticks; 1 photographed), *B. contaminata* (few ♂♂), *P. flavescens* (few soaring), *R. phyllis* (few soaring), *D. trivialis* (few on the road), *D. nebulosa* (few, mostly males, in emerging grass), *Neurothemis fulvia* (a male on a bush), *Hydrobasileus croceus* (a male flew twice across the same gap between bushes

Figure 55. Copula of Ischnura senegalensis **on a bladdenworth (**Utricularia **cf.** aurea**, but with unusually inflated floats) in inundated scrub 9 km SE of Siem Reap (Loc. WF4), 12.12.2019.**

and disappeared). In December 2019 dragonflies also appeared less diverse than in November 2018: very many *B. contaminata*, many *O. servilia*, *T. pallidinervis*, few *D. trivialis*, *D. nebulosa*, *O. sabina*, *P. flavescens*, solitary *P. congener* (a young male) and *T. tillarga*. At this time, males of both *P. flavescens* and *D. trivialis* were reproductively active, that is not too often observed for these widespread species. The former coursed over the water and even chased each other; the latter (all blue) perched on emerging stems (but did not keep to the same perch), were cautious and flew fast and far when startled. That was so dissimilar to the 'normal' and habitual behaviour of non-breeding males which rest on barren ground, are not cautious and fly for very short distance.

Swamp between Phnom Krom and Sambuor villages (PK)

In 9.9 km to SW of the Siem Reap City centre there is a sharp rocky hill called Phnom Krom (Figs 58-59) (Khmer: Lower Mountain; 13.28-29 N, 103.81-82 E) with Prasat Phnom Krom Temple, built at the end of 9th century, on its top. The hill foot is narrowly surrounded by Phnom Krom village and further with vast rice fields (Fig. 58-59). These are completely inundated during the high level season (Figs 58, 59, bottom photo), while in the low level season the water front is 5 km to the south. In 700 m north of the hill foot (13.2940 N, 103.8140 E), a high embankment, with an elevated ground road upon, starts and goes to the west and then to north-west. The state of the road in November suggested it had been inundated at the highest lake level. The embankment serves as a dam of a 3 x 2 km water reservoir aimed to feed the rice fields at its S/SW side. It is much deeper than other reservoirs along the northern lake bank, being a huge

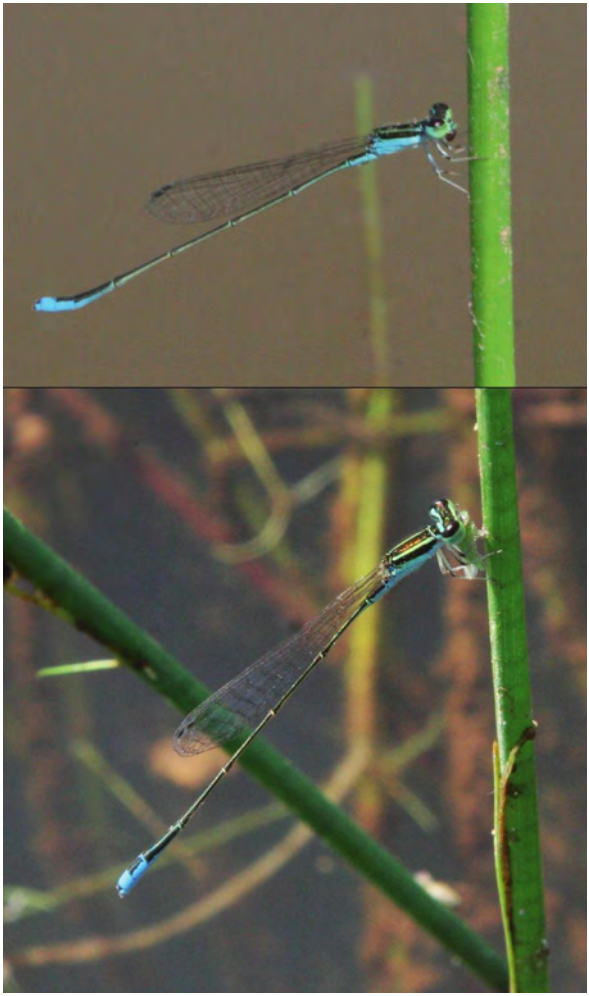


Figure 56. Males of Aciagrion borneense **in sparse emerging grass in inundated scrub 9 km SE of Siem Reap (Loc. WF4), 05.11.2018. The photographed male(s) and one collected male of** A. borneense **had S9 entirely blue, as usual for the species, but three collected males had a narrow black dorsal streak throughout it. Laidlaw (1924) admitted possibility of dorsal black marking on S9 in males this species.**

swamp thickly overgrown with floating vegetation which from distance would look as a meadow if people would not move across it by boats (Fig. 60, the second photo from bottom). In 4 km NW from Phnom Krom (13.3128 N, 103.7905 E), the embankment forks and the right branch goes through the swamp western margin northwards to Sambuor village (13.33 N, 103.80 E). The swamp attracts Openbill Storks and other birds and is full of all kinds of wildlife. The depth and other conditions of this swamp do not change during the season as much as in other areas near the lake. At the late low season, bulrush (*A. grossus*) patches (but not too large) appear at the 'rice side' of the embankment. The swamp margin along the embankment was studied on 26.02.2017 (11:30 a.m. - 1:20 p.m. and 4 - 6 p.m.) and 01.03.2017 (5 - 6 p.m.) in early low season, 18.06.2018 (11 a.m. – 1 p.m.) in late low season, 03.11.2018 (5:10 - 6 p.m.) and 05.11.2018 (12:40 a.m. – 1:30 p.m.) in high season, and 12.12.2019 (4 – 5:20 p.m.) in late intermediate season. In sum 24 species registered.

PK1. (20 species) The deep swamp part from the start of the embankment to its fork: 13.294-313 N, 103.791-814 E (with the preferred section 13.302-306 N, 103.791-794 E; 2.8- 3.4 km NE of Phnom Krom). The SE corner of the swamp closest to Phnom Krom is more than a hu-

Figure 57. Males of Paracercion calamorum **perching at open water: a – in shallowly inundated scrub 4.5 km NNW of the Phnom Krom hill (Loc, PK2), 26.12.2017**; **b – in inundated scrub 9 km SE of Siem Reap (Loc. WF4), 5.11.2018.**

man height deep, has some areas of open water alternating with water hyacinth carpets (Figs 10 (two top photos), 60). Further to northwest the water becomes about waist-deep and filled with some semiaquatic Poaceae grass with very thin leaves, abundant *Salvinia cucullata* and some *Nymphoides indica* and *Ottelia* sp., while the higher level is dominated with tall lotus (*Nelumbo nucifera* Gaertn.) (Figs 61-63). The grass (well seen in the lower photo of Fig. 63) forms a floating bog, upon which it was possible to move by 'crawling' but by neither walking nor swimming. Sparse low trees and bushes (partly dead), as usual covered by ivy woodrose, rise from the water (Fig. 63). There are lines of 'normal' trees and bushes aside the embankment road where many larger dragonfly concentrate.

In accordance with less profound seasonal changes of this habitat, the odonate assemblage did not change much as well, as I do not think the below reported fluctuations reflect some regular seasonal cycles. Large dragonflies, concentrated at the embankment, were represented by *C. servilia* (quite many in February (1 ♂ photographed) and, mostly females, in June, very many in November and December), *T. pallidinervis* (very many in February, not registered in June, quite many in November and December), *U. signata* (many in February (1 ♂ photographed – Fig. 40b), few

Figure 58. Phnom Krom Hill 9.9 km SW of Siem Reap in the high water season. The two top photos represent an unusually high lake level in November 2011. Photos by Eddie Smith.

in June, not registered in November, 1 ♂ seen in December), *O. sabina* (few in June, many in November, no in December). *R. rufa* (registered only in June, many males on the water invariably with lotus, females at embankment bushes, 1 ♂ (Fig. 41b), 1 ♀ (Fig. 42b) photographed), *R. phyllis et variegata* (as usual always on the wing; few in February, very many in June, 3 ♀♀ of *R. variegata* in November, not seen in December), *P. flavescens* (1 territorial ♂ in November, many in December), *T. tillarga* (few commenced a twilight flight in February). Of smaller dragonflies, *B. contaminata* was numerous and dominated among small dragonflies in all seasons, it kept to windows of open water and avoided thick lotus thickets. *A. panorpoides* and *D. nebulosa* (both photographed – Figs 64-65) occurred at lotus thickets and less readily at the water hyacinth matts: both were numerous in February, in June the former was frequent but the latter not seen, in November none of the former and many of the latter were seen, in December one individual of the former and quite a few of the latter were observed. In February few males and in November one male of *B. chalybea* occurred in the same floating vegetation habitats. A male of *D. trivialis* was met in February in grass at the embankment. Two males and a female of *N. tullia* were seen at bulrush in June and one male at water hyacinth in November. *A. aethra* was observed only in June: a male (Fig. 35c) and female (Fig. 35b) (photographed) close to each other on lower branches of a bush on the embankment and a male on a water hyacinth matt.

Of damselflies, *Agriocnemis* spp. were expectedly found on the water, especially in fine grass, but were few in February (*A. minima* and *A. pygmaea*, the latter represented by one female) and June (*A. minima*; 1 ♀ photographed), not seen in November but numerous in December (seemingly all *A. minima*; 4 ♂♂ collected). *I. senegalensis* was not too rare in December but otherwise only a male and female were seen in February. Such solitary findings were also made as a male of *C. cerinorubellum* (collect-

Figure 59. Phnom Krom Hill (middle) and rice fields nearby: top and middle – at the low water season (26.02.2017 and 22.02.2017, respectively); bottom – at the high water season (3.11.2018).

ed) in the grassy floating bog in February and a male of *P. australasiae* in November.

PK2. (16 species) The right arm of the embankment from its bifurcation for 1-1.5 km to the north (at this section with a line of young eucalypts): 13.313-321 N, 790-793 E, 4-4.8 km NNW of Phnom Krom. The water, now at both sides of the embankment becomes shallower (its level strongly changes during the season), with a silty but not sucking bottom. Aquatic vegetation became scarce and regular seasonably flooded scrub appears (Fig. 66). Macrophytes were represented by *Utricularia* sp. (a lot in February), *Nymhpaea* sp., *N. indica* and *Rotala* sp. (many in November, see bottom photos of Fig. 66); the water hyacinth occurred at deeper places at bushes. Examined on 26.02.2017 and 05.11.2018. Dragonflies: *O. sabina* (both times numerous); *C. servilia*, *D. nebulosa* (few in February, many in November), *B. contaminata*, *T. pallidinervis* (many in February, few in November), *R. variegata* (both times frequent), *U. signata*, *R. phyllis*, *P. flavescens* (frequent in February),

Figure 60. The water hyacinth carpet in a huge swamp 1-2 km NW of Phnom Krom Hill (Loc. PK1); the second photo from bottom of 12.12.2019, others of 1.11.2018.

D. trivialis (few in February on the solid ground).

Of damselflies, in February only quite frequent males (1 collected) of *P. calamorum* were observed, perching on solitary floating leaves of bladdenwort or water lily (Fig. 57a). In November they were rather fewer but there were also *A. borneense* (quite a few ♂♂ in sparse emerging grass), *I. senegalensis* (quite a few ♂♂, few ♀♀), *P. australasiae* (few ♂♂ and ♀♀; 1 ♂ and 1 ♀ collected), *P. rubriceps* (2 ♂♂, 1 photographed – Fig. 49c) and *A. minima* (1 ♀).

Merchey

To the west of Siem Reap, opposite to the SW corner of West Baray, a road branches off the National Highway No.6 to SW and goes to Merchey village which is connected by a canal to the lake and so serves as one of the two water gates leading to the Stung Sangkae River mouth, which numerous birdwatchers visit. We visited Merchey (13.358 N, 103.717 E) shortly on 01.11.2018 and found the land inundated, with big water spaces between bushes where water hyacinth matts floated. We examined a short section of some ground road which was just appearing from the water at the village but still inundated further to the west (Fig. 67). There were numerous *B. contaminata* and *D. nebulosa*, many *C. servilia* (all females; even immature yellow males were absent but I noticed some orange dragonfly of a relevant size), *N. tullia*, *D. trivialis*, *O. sabina*, and I saw a soaring *P.*

Figure 61. The floating bog dominated by lotus in a huge swamp 2-3 km NW of Phnom Krom Hill (Loc. PK1); the second photo from bottom of 18.06.2018, others of 26.02.2017.

flavescens, an active male of *T. tillarga* and (already from inside a car) a tiny yellowish damselfly (*?I. aurora*) flying by. Eight species.

Prek Toal (PT)

Prek Toal (Preaek Toal) is a Cham floating village (Kaoh Chiveang Commune, Aek Phnum District, Battambang Province) (Fig. 68) at the Stung Sangkae River near its mouth which the Osmose Community Project has made the first must see (and hence quite expensive) place for birdwatchers in Cambodia as a base of the Prek Toal Bird Sanctuary, a Ramsar Convention site. All published data on Odonata of Lake Tonle Sap (Benstead 2006; Roland & Roland 2010; Roland et al. 2011; Seehausen et al., 2016) originated from this place. I visited it only on 10.12.2019, arriving there by a big boat and examining the village closest surroundings (13.230-233 N, 103.665-670 E) using a small flat-bottomed boat from 1:30 to 2:30.

The river mouth (Figs 11, 69) was marked with thickets of the Giant Cane (*Arundo donax*), still inundated but with ca 1 m of stem length recently released from water and still having no leaves. They included some bushes of Giant Sensitive Tree (*Mimosa pigra*) and few tall trees. At the village, the river course was also marked

Figure 62. The floating bog dominated by lotus (Nelumbo nucifera**) and participation of** Nymphoides indica, Salvinia cucullata **and Poaceae gen. sp. in a swamp 2-3 km NW of Phnom Krom Hill (Loc. PK1), 05.11.2018.**

by lines of cane and bushes, behind which there were 'bays', of different size, of more open water among denser *A. donax* and *M. pigra* bushes. At the base of bushes and cane, water hyacinth was concentrated and the flowering morning glory (*Ipomea aquatica* L.) was frequent. The depth was mostly more than 2 m but in some places the bottom was reachable. Everywhere *B. contaminata* was present in immense numbers, males of *C. servilia* frequently occurred and one male of each *O. sabina, N. tullia,* and *D. nebulosa* were seen in the water hyacinth zone and a male of *U. signata* in the cane zone at the mouth. Quite surprisingly, there was not any *T. pallidinervis*. The most numerous damselfly, with frequent tandems, was *P. rubriceps* (3 ♂♂ 1 ♀ collected), less frequent were males of *P. microcephalum* (4 collected) and I. senegalensis (1 ♂, 1 orange ♀ collected). Interestingly, all these damselflies mostly occurred at the 'banks' (with water still more than 2 m deep) of the main river course, marked by cane and *M. pigra* bushes, but were scarce in 'bays'. At those 'banks', few males of *C. auranticum* (1 collected) were also met while in a 'bay' an immature, still red female of *Agriocnemis femina* was collected (the only one at the lake at all).

In total 11 species registered by me (but 22 together with the literature data).

Road from Mukh Paen to Sangkae River (MP)

During the high water season, Lake Tonle Sap increases its area partly in expense of the huge floodplain of the Stung Sangkae and smaller river entering it at its NW end.

Figure 63. Low trees in a lotus swamp 3 km NW of Phnom Krom Hill (Loc. PK1); the dates from top to bottom: 18.06.2018, 26.02.2017, 26.02.2017, 05.11.2018, 12.12. 2019.

It is some 50 km long and 35 km wide and is mostly covered by low seasonably flooded forest and scrub. The best way to examine that floodplain was to penetrate it via a 16 km long elevated road (well seen even from a plane, see Fig. 9) starting at the remarkable Big Tree (13.4720 N, 103.6088 E) at the S margin of Mukh Paen village (Mukh Paen Commune, Puok District, Siem Reap Province) and proceeding SW to a village on the Sangkae River banks (13.3481 N, 103.3279 E). The exact name of that village is unclear: in two different tourist maps it is indicated as Pou Treay or Chheu Kmau while is nameless in Google Earth. It is only clear that it is situated (like Prek Toal) in Kaoh Chiveang Commune, Aek Phnum District, already in Battambang Province. Since the sites examined resided in Siem Reap Province, I designate them 'MP' after Mukh Paen village.

This area was visited on 03.12.2019 and 13.12.2019 (both times from 10 a.m. to 2 p.m.), in the late mid-water season. Although the road still showed signs of very recent inundation (very bad but being repaired), the water had actually withdrawn from vast scrub of the floodland back to the river's very banks, having left a sticky wet ground. On the way from Mukh Paen village to the river, the road, as usual accompanied by a canal, crosses the following terrain: (i) overgrazed pastures, (ii) rice fields, (iii) dry wasting land with regenerating scrub (until this level the land seemed not be reachable by the lake high water), (iv) inundated scrub on the E side and rice field on the W side, (v) inundated forest composed by low trees braided with ivy

Figure 64. A male of Acisoma panorpoides **in a lotus swamp 3 km NW of Phnom Krom Hill (Loc. PK1), 26.02.2017.**

Figure 65. A male of Diplacodes nebulosa **in a lotus swamp 3 km NW of Phnom Krom Hill (Loc. PK1), 26.02.2017.**

woodrose (Fig. 70), (vi) large area of inundated grass (Fig. 71) (vii) non-inundated scrub at both sides, (viii) vast open areas with fine grass, solitary big trees and large shallow ponds (with a lot of water buffaloes and big flocks of open bill storks), currently with very wet sticky ground (Fig. 72), (ix) thick scrub with the same wet ground.

Figure 66. Inundated scrub at the NW corner of a huge swamp, 4.5 km NNW of Phnom Krom Hill (Loc. PK2); top photo of 26.02.2017, others of 05.11.2018. On the two lower photos numerous emerging Rotala **sp. with lilac inflorescences is seen.**

There was no possibility to study the river banks since they were completely occupied with the (very dirty) fishing village. There was a lot of water hyacinth along the bank but no other vegetation. Generally the river looked the same as at Prek Toal, differing only in having firm banks.

So I briefly studied three sites in zones (v), (vi) and (vii), considered below in the reverse order in line with the adopted principle 'from water to inland'. They were situated close to each other (within 1.7 km of the road, see Fig. 9) and differed as damselfly habitats while dragonflies were mostly the same, so I do not include them in Table 1 as separate entries. In sum, 19 Odonata species were registered.

MP1. The channel banks, scrub with wet ground and a considerable roundish reserve enclosed with low dams with trees; 13.396-398 N, 103.564-565 E. Examined at 12 a.m. -1:30 p.m. on 03.12.2019 and at ca 10:30 and 12 a.m. on 13.12.2019. Dragonflies were as follows: very numerous - *C. servilia* (but not too many mature red males) (Fig. 73, left); numerous - *O. sabina* (mostly at bushes), *B. contaminata* (at water); less numerous - *T. pallidinervis* (on sticks near the canal) (Fig. 73, right); frequent - *P. flavescens*

Figure 67. Inundated scrub and a road being released from water at Merchey village (Loc. M), 01.11. 2018.

Figure 68. Prek Toal floating village at the Sangkae River mouth (Loc. PT). 10.12.2019.

Figure 69. Inundated vegetation (mostly of alien species, Giant Cane and Giant Sensitive Tree) at the Sangkae River mouth (close to Loc. PT). 10.12.2019.

(soaring), *R. variegata* (fluttering), *D. trivialis* (at the canal); solitary – a male of *D. nebulosa*, a male of *N. fulvia* (both at the roundish reserve), a young male of *P. congener* (a male in scrub), *T. tillarga* (startled from bushes). On 03.12.2019 above a secondary road at the roundish reserve a mixed swarm was observed which included several *P. flavescens*, four *R. variegata* and one *R. phyllis*. No damselflies at this place.

MP2. A large, 700 x 400 m, knee-deep swamp filled with fine Poaceae grass (like at PK1) (Fig. 71), including a lot of *Salvinia cuniculata* and *Utricularia* sp. (but no lotus or water snowflake). Partly examined at 13.401-402 N, 103.566-567 E, at 12:10-13:20 a.m. on 13.12.2019. Of dragonflies, there were numerous *D. nebulosa* and frequent *O. sabina* while *B. contaminata* was represented by two males only. There was a male of *R. phyllis* which ranged to and fro above the water, that is patrolled a territory, unlike to fluttering in swarms so habitually observed for both sexes of this species and *R. variegata*. Damselflies were represented mostly by *I. senegalensis* while others were scarce: quite a few males and a tandem (collected) of *P. australasiae* at windows of open water (its males seem to tend to more actively and far flying over open water than those of other congeners), several females of *A. minima* (two collected) and one male of *A. borneense* (collected).

MP3. A waist-deep swamped margin of the inundated forest (Fig. 70) along the road; ca 13.406 N, 103.573 E (exact coordinates uncertain). Examined at ca. 1:40-2 p.m. on 3.12.2019. There were many

Figure 70. Inundated low forest on the Stung Kae/Tonle Sap floodplain ca 6 km SW of Mukh Paen village (Loc. MP3) at the intermediate water season, 13.12.2019.

Agriocnemis, of which 1 ♂ 3 ♀♀ of *A. minima* and 1 ♀ of *A. pygmaea* were collected, several *P. rubriceps* of both sexes, two females of *I. senegalensis* (1 orange ♀ collected) and a male of *P. australasiae* (collected). Also a male of *N. tullia* (without milky stripes on the wings, the condition of males developed in the dry season) was met.

Tonle Sap River in Phnom Penh (PP)

Although Phnom Penh is situated 116 km SSE off the Lake Tonle Sap SE end, it resides at the mouth/source (depending on the season) of the Tonle Sap River, the broadening of which the lake is, so it is reasonable to include here the Phnom Pehn observations made on 28.02.2017. In Phnom Penh, the river is enclosed to concrete so that natural vegetation is represented by only sparse and small patches of water hyacinth, and a lot of rubbish are everywhere at the banks. Just upstream the Royal Palace (11.568 N, 104.931 E) I found a small patch of a ground bank with some grass and small *Miscanthus* sp. thickets. There I saw very many *B. contaminata*, few *D. trivialis*, a male of *O. sabina* on the ground and a male of *T. pallidinervis* on a *Miscanthus* stem. This set was the same as would be met in similar conditions at the lake.

At the level of the Tonle Sap and Mekong junction, next to Himawari Hotel (11.559 N, 104.938 E), there is a patch of a gentle ground bank with green grass in which I found a male of *A. pygmaea* and two rare damselfly species: not less than three males of *I. aurora* and a male of *Amphiallagma parvum* (for my 13 visits to Cambodia I found this species only thrice).

In sum 7 species.

Figure 71. A big area of knee-deep inundated fine grass on the Stung Kae/Tonle Sap floodplain ca 8.5 km SW of Mukh Paen village (Loc. at the intermediate water season, 13.12.2019.

Figure 72. Open areas with sparse trees, being released from water, on the Stung Kae/Tonle Sap floodplain ca 15 km SW of Mukh Paen village at the intermediate water season, 13.12.2019.

Figure 73. A female of Crocothemis servilia **(left) and** Trithemis pallidinervis **(right) at the bank of the canal ca 7.5 km SW of Mukh Paen village (Loc. MP1), 03.12.2019.**

Curiously, that specimen of *A. parvum* (Fig. 74a) has its back side of the head blue entirely rather than with a blue butterfly-like shape as common for this species (Fig. 74b), otherwise fitting the species perfectly.

A note on Amphiallagma parvum

Beyond the above reported male, I collected this species in Cambodia twice: in Ban Lung, Ratanakiri Province (2 males) (Kosterin 2016) and at Choum Thom forest swamp in Prey Long Forest in Preah Vihear Province (also two males) (unpubl.). Those males had the occiput blue below and black above, with two narrow blue postocular spots on the black part, confluent to the blue of the low part and so forming a blue butterfly-like shape (Fig. 74b), more or less fitting the above descriptions by Fraser (1933). In contrast to them, the Phnom Penh male has the occiput entirely blue (Fig. 74a).

The latter condition corresponds to the original description of this species (by one male from India without further detail): "Face bleuâtre clair, y compris le devant des premiers articles des antennes, sans marques obscures distincte. Le dessus de la tête noir; taches postoculaires bleues, grandes, cunéiformes, immédiatement suivies en arrière par la couleur pâle, sans être délimitées de ce côté par du noir". [Light bluish face, including the front of the first antennae articles, without distinct obscure marks. The top of the head black; blue, large, cuneiform postocular spots, immediately

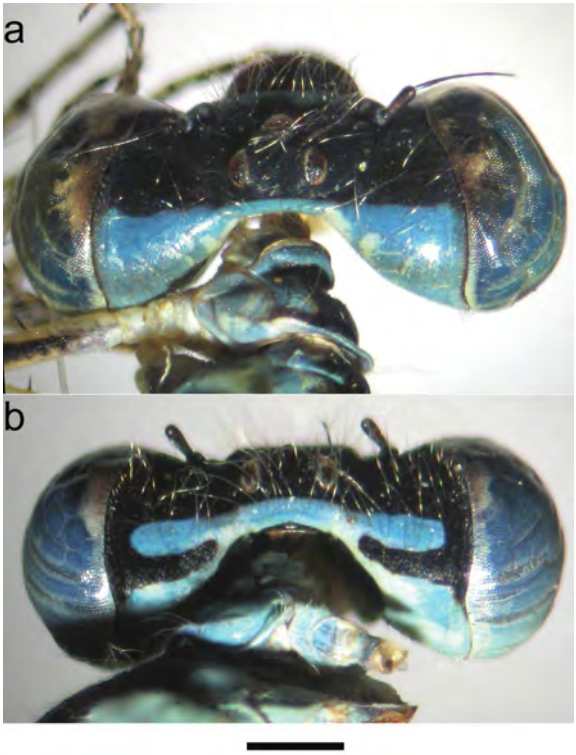


Figure 74. Heads of males of Amphiallagma parvum**: a – Phnom Penh centre, the Mekong River right bank at the ferry, 28.02.2017**; **b – Preah Vihear Province, 4.5 km WSW of Spong village, Lake Boeng Pes, 13.447-448 N, 105.505-506 E, 8.12.2019. Scale bar 0.5 mm.**

followed behind by the pale colour, without being delimited on this side by black] (Selys 1867: 536).

On the other hand, the description (from 'Sonder Bhandara, Central Provinces [of India]) of *Ischnura immsi* Laidlaw, 1913, a junior subjective synonym of *A. parvum* (Fraser 1933), reports the 'butterfly shape': "but the nasus black; upper surface velvety black, a linear postocular mark on either side, blue, meeting its fellow in the middle line" (Laidlaw 1913: 236). Note also the difference with Selys (1876) in the colour of anteclypeus. In contrast to Selys (1867), Fraser (1933: 376) also reported "postclypeus black or broadly black at base".

Fraser (1933) reported female dimorphism in *A. parvum* which also concerns the occiput coloration where it was not well explained: with the postocular spots either 'enclosed' or not. Less explicitly, he also hinted at existence of dimorphism in the occiput coloration in males, as follows: "vertex and occiput black, the latter with small postocular spots confluent across the middle line by a narrow occipital stripe" (Fraser 1933: 376), versus "In some specimens of the male the postocular spots are bordered narrowly with black behind, but the central stripe not so, so that the spots are narrow gulfs opening on to the blue at the back of the head" (Fraser 1933: 378). It is clear that although both statements were opposed by the expression "in some males", they describe the same 'butterfly shape', so it remains unclear what the alternative was implied, perhaps the entirely blue occiput. Moreover, it can be reconstructed that Fraser made lapsus calami and was going to say that in those 'some males' this alternative condition was found, since they were obviously implied to have a restricted black pattern: "In these specimens, also, the black on the postclypeus is restricted to its base, and the anterior collar of the prothorax is blue. The description of the type, writ-

ten, apparently, from a teneral specimen, approaches this condition, which is similar to that of the heterochromatic female, as the postclypeus is unmarked with black and the post ocular spots and stripes are unenclosed with black behind." (Fraser 1933: 378).

In iNaturalist.org there are 13 photographic observations of *A. parvum* showing the occiput. It has the 'butterfly-shape' in 10, in one the black 'enclosing' is very faint and in two the occiput is entirely blue. All the last three observations are from West Bengal, along with 7 others from there showing the 'butterfly shape'. Bedjanič et al. (2014) provided a photo of a male of *A. parvum*, from India with narrow black lines 'enclosing' the postocular spots to separate them from the blue below.

Few images and specimens available suggest that the 'butterfly shape' is common (14 cases), the entirely blue occiput is less frequent (3 cases) and the intermediate type with narrow black stripes is further less frequent (2 cases). This looks like an imperfect dimorphism or continuous variation. The black on the postclypeus is normal and its absence probably unusual.

Discussion

The registered fauna of Odonata at Lake Tonle Sap is rather scarce as counting just 41 species, so the above given ecological information, although difficult to generalise, makes more sense than the faunal data. To sum them up I provide in Table 1 a checklist of species with indication of localities where they were found by me, and in Prek Toal also by previous authors. Table 1 contains also subjective codes of abundance, relevance of which, as well of the species' presence as such, is limited by the fact that only three main localities, Kampong Pluk environs (PK), the road to the watermelon field (WF) and the swamp between Phnom Krom and Sambuor (PK) were examined on both high level season of the lake (November) and the low level season (February/March and June).

Only four odonate families are represented: Coenagrionidae (16 species), Gomphidae (3 species), Macromiidae (1 species) and Libellulidae (22 species, more than half). If not to consider Merchey and Phnom Penh, which were not studied properly, six species (all libellulids), *B. contaminata*, *C. servilia*, *O. sabina*, *R. phyllis*, *T. tillarga* and *T. pallidinervis*, were registered in all main localities and eleven species, *A. femina*, *A. nana*, *C. cerinorubellum*, *I. aurora*, *M. phalantus*, *S. clavatus* (not seen by me), *E. frontalis*, *A. brevipennis*, *O. sabina*, *H. croceus*, *P. jorina* were registered in one main locality only.

The species thriving and omnipresent at the lake banks themselves is *B. contaminata*, perhaps because of its ability to develop in both clear and turbid water and a habit to keep to open water and floating vegetation. Everywhere it was accompanied, but in much less numbers, by *O. sabina* and to some extent *C. servilia*. Two congeneric damselfly species feel at home on the floating vegetation (mostly water hyacinth) at the lake and Stung Sangkae River, *P. microcephalum* and *P. rubriceps*. Curiously *P. microcephalum* was confined to the lake itself and even at the end of the low season was found only at its bank (loc. WF1), while the very similar in appearance *P. australasiae* was never found at the lake itself but occurred over shallow water of inundated scrub further inland (WF4, PK1, PK2), where *P. microcephalum* was not in turn found. At least in Cambodia, these two species tend to exclude each other, however they can be found in the same habitats as well (Kosterin 2019b). A number of dragonfly species are very abundant at the lake banks near tall bushes of *M. pigra*, either inundated or not:

T. pallidinervis and *U. signata* (the former more frequent), which perch on protruding branches, and *R. phyllis* and *R. variegata* (most probably conspecific, see Kosterin 2010), which flutter among them. *T. tillarga* is abundant at the forest and scrub facing the lake, inundated or not, seemingly at any season. Other species at least once found at the immediate lake bank are *A. nana*, *C. praetermissum*, *I. senegalensis*, *M. phalantus*, *A. aethra*. The latter seemed out of place at a huge water body and probably arrived from some nearby smaller pool filled with water hyacinth. All the above mentioned species but *M. phalantus* and *A. aethra* are very common lentic species elsewhere in the Oriental ecoregion. For some reason I have never seen *P. flavescens* at the lake banks as such.

The rest of the revealed fauna is represented by widespread lentic species registered with various abundance (up to a single individuals, viz. *A. femina*, *A. nana*, *C. cerinorubellum*, *B. sobrina*, *H. croceus*) at various water bodies of the land periodically inundated by the lake water.

Interestingly, at the Stung Sanngkae River mouth at Prek Toal village, the overwhelming majority of damselflies occurred at the lines of water hyacinth at the base of the giant cane and giant sensitive tree marking the main river course, although still inundated by water more than 2 m deep, but were scarce in lateral 'bays' among these thickets, with seemingly the same conditions. This looked strange since the water of the main course was permanently disturbed by big motor boats (Fig. 68) so that the water hyacinth patches inhabited by these damselflies were repeatedly and severely shaken by waves, while the 'bays' were calm. I even suppose that it was this water shaking that attracted damselflies. For instance, according to my observations, the common northern Eurasian species *Erythromma najas* (Hansemann, 1823) is a predator specialised to hunt for small insects fallen to water: it perches on sparse floating plants among open water and makes shot flights towards sources of the surface oscillations. Those Cambodian damselflies which spend most of their life at floating water hyacinth may have the same trophic instincts. As a result, they eventually concentrate at those water hyacinth patches which undergo most shaking because of boats.

I would like to point out a useful cue for recognition in the field of very similar, saturated red mature males of *C. servilia* and *R. rufa* (females of which are so different). The former perch on top of stems and branches (Fig. 36a-b)while the latter invariably perch orienting their abdomen along a branch or stem (Figs 41) (besides, the colour of their abdomen looks a bit uneven). The conspicuous females of *R. rufa* often sit flat on leaves of bushes or low trees (Fig. 42a).

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Table 1. Checklist of Odonata of Lake Tonle Sap, with indication of localities and sublocalities were they were found by me (for the codes see the text), or previous authors which are encoded as follows: B – Benstead 2006; RR – Roland & Roland (2010); RSR – Roland et al. 2011; SCS – Seehausen et al. 2016. Codes for subjective relative abundance are given in parenthesis after (sub)localities as follows: 1 – single individual found, 2 – few (2 to 5) individuals observed, 3 - moderately abundant (6-20 seen), 4 – abundant (~20-100); 5 – very abundant (hundreds). If a locality was visited in more than one season, a range of relative abundance is given, where 0 means a species was not observed on at least one seasonal examination (so one value provided most probably means that the locality was visited once rather than the species had stable abundance). Merchey is not included as examined too shortly.

	localities	KK		KP			WF				PK		PT	MP	PP
No	sublocalities species	KK1	KK2	KP1	KP2	KP3	WF1	WF2	WF3	WF4	PK 1	PK2			
1	*Aciagrion borneense* Ris, 1911	-	-	-	-	-	-	-	-	0-4	-	0-2	-	1	-
2	*Amphiallagma parvum* (Selys, 1876)	-	-	-	-	-	-	-	-	-	-	-	-	-	1
3	*Agriocnemis femina* (Brauer, 1868)	-	-	-	-	-	-	-	-	-	-	-	-1	-	-
4	*Agriocnemis minima* Selys, 1877	-	-	-	3	3	-	0-1	-	0-1	0-4	0-2	- RSR, SCS	3	-
5	*Agriocnemis nana* (Laidlaw, 1914)	1	-	-	-	-	-	-	-	-	-	-	-	-	-
6	*Agriocnemis pygmaea* (Rambur, 1842)	-	-	-	3	0-3	-	0-3	0-2	0-1	0-2	-	- B	1	1
7	*Ceriagrion auranticum* Fraser, 1922	-	-	-	-	-	-	0-3	-	-	-	-	2 SCS	-	-
8	*Ceriagrion cerinorubellum* (Brauer, 1865)	-	-	-	-	-	-	-	-	-	0-1	-	-	-	-
9	*Ceriagrion praetermissum* Lieftinck, 1929	-	-	0-1	-	0-3	-	0-3	-	-	-	-	-	-	-
10	*Ischnura aurora* (Brauer, 1865)	-	-	-	-	0-2	-	-	-	-	-	-	-	-	2
11	*Ischnura senegalensis* (Rambur, 1842)	-	-	-	2	1-3	2	0-1	0-2	2	0-3	0-2	3 SCS	3	-
12	*Paracercion calamorum dyeri* (Fraser, 1919)	-	-	-	-	-	-	-	-	0-4	-	2-3	-	-	-
13	*Pseudagrion australasiae* Selys, 1876	-	-	-	-	-	-	-	-	0-2	-	2	-	2	-
14	*Pseudagrion microcephalum* (Rambur, 1842)	3	-	0-3	-	-	2	-	-	-	-	-	3	-	-

	localities	KK		KP			WF				PK		PT	MP	PP
No	sublocalities species	KK1	KK2	KP1	KP2	KP3	WF1	WF2	WF3	WF4	PK 1	PK2			
15	*Pseudagrion rubriceps* Selys, 1876	3	-	0-4	0-2	-	1	-	-	0-1	-	0-2	4 RSR	2	-
16	*Ictinogomphus decoratus melaenops* (Selys, 1858)	-	-	0-1	2	-	2	-	1	-	-	-	- RSR	-	-
17	*Macrogomphus phalantus jayavarman* Kosterin, 2019	-	-	0-3	-	-	-	-	-	-	-	-	-	-	-
18	*Sinictinogomphus clavatus* (Fabricius, 1775)	-	-	-	-	-	-	-	-	-	-	-	- SCS	-	-
19	*Epophthalmia frontalis* Selys, 1871	-	-	0-3	-	-	-	-	-	-	-	-	-	-	-
20	*Acisoma panorpoides* Rambur, 1842	-	-	-	1	0-3	-	0-1	-	-	0-4	-	- B, RSR	-	-
21	*Aethriamanta aethra* Ris, 1912	-	-	0-1	-	-	-	0-3	-	-	0-2	-	-	-	-
22	*Aethriamanta brevipennis* (Rambur, 1842)	-	-	-	-	-	-	0-2	-	-	-	-	-	-	-
23	*Brachydiplax chalybea* Brauer, 1868	-	-	-	1	0-1	1	1	-	-	0-2	-	-	-	-
24	*Brachydiplax sobrina* (Rambur, 1842)	-	-	-	-	0-1	-	-	-	-	-	-	-	-	-
25	*Brachythemis contaminata* (Fabricius, 1793)	3	4	4-5	4	3-4	5	5	1-4	2-4	4	2-3	4 RR, RSR, SCS	4	4
26	*Diplacodes nebulosa* (Fabricius, 1793)	-	-	-	-	0-4	-	-	0-1	2	0-4	2-3	2	3	-
27	*Diplacodes trivialis* (Rambur, 1842)	-	-	-	1	0-3	-	0-2	1-2	2	0-1	0-2	- RR	3	2
28	*Crocothemis servilia* (Drury, 1770)	-	3	2-3	3	0-4	3	1-4	0-3	3-4	3-4	2-3	3 SCS	4	-
29	*Hydrobasileus croceus* (Brauer, 1867)	-	-	-	-	-	-	-	-	0-1	-	-	-	-	-
30	*Neurothemis fulvia* (Drury, 1773)	-	-	-	-	-	-	-	-	0-1	-	-	-	1	-
31	*Neurothemis tullia* (Drury, 1773)	-	-	-	3	0-4	-	-	-	-	0-2	-	1 SCS	1	-
32	*Orthetrum sabina* (Drury, 1770)	3	-	2-4	2-3	2-4	-	1-3	0-3	2-4	0-3	3	1	4	1

	localities	KK		KP			WF				PK		PT	MP	PP
No	sublocalities species	KK1	KK2	KP1	KP2	KP3	WF1	WF2	WF3	WF4	PK 1	PK2			
33	*Pantala flavescens* (Fabricius, 1798)	-	1	-	2	0-1	-	-	0-1	2	0-3	0-3	- SCS	3	-
34	*Potamarcha congener* (Rambur, 1842)	-	-	-	-	-	-	-	-	0-1	-	-	-	1	-
35	*Pseudothemis jorina* Förster, 1904	-	-	2	-	-	-	-	-	-	-	-	-	-	-
36	*Rhyothemis phyllis* (Sulzer, 1776)	2	2-4	-	3	0-2	1	-	0-3	0-2	0-4	0-3	- SCS	2	-
37	*Rhyothemis variegata* (Linnaeus, 1763)	-	-	2-4	3	0-2	1	0-1	0-3	-	0-4	3	- SCS	4	-
38	*Rhodothemis rufa* (Rambur, 1842),	-	-	-	3	0-1	-	-	0-2	-	0-3	-	-	-	-
39	*Tholymis tillarga* (Fabricius, 1798)	3	-	4	-	0-2	-	-	-	1-4	0-2	-	- RSR	1	-
40	*Trithemis pallidinervis* (Kirby, 1889)	1	1	0-3	-	0-4	-	0-3	0-3	3-4	0-4	2-3	- RSR	4	1
41	*Urothemis signata* (Rambur, 1842)	1	1	0-1	3	-	-	0-2	-	-	0-3	0-3	1 SCS	-	-
	totally	11		28			30				24		22	19	7
		9	6	15	17	20	9	16	13	19	20	16			