

Review of the observations of aggregates of Steninae reported since 1856 (Coleoptera Staphylinidae)

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ABSTRACT

The nine aggregates of Steninae documented since 1856 are reviewed, completed with seventeen new reports. All the pictures available on the topic are presented. Considering the ubiquity and megadiversity of the subfamily, this total of 26 observations reported over the last 150 years appears strikingly low, clearly indicating that the phenomenon is exceptional. These observations were all made in the Palaearctic and Oriental realms, and refer to both the extant genera of Steninae *Dianous* and *Stenus*. Six observations refer to *Dianous* species, all from China, mainly *D. banghaasi* and *D. freyi*. Of the twenty observations referring to *Stenus* ten were made in the Mediterranean area, mainly on *S. cordatus*, *S. elegans* and *S. turk*. This collection of observations seems a composite of several kinds of behavioural patterns, such as hibernation, aestivation, reproductive swarming, and possibly hilltopping, with some most likely intermixed. Aggregation in compact multilayer masses of individuals as well as occasional recurrence of *Stenus* aggregates at precise locations over days or year are probably controlled by pheromone signals. The reasons driving these slender, one centimeter long rove beetles to occasionally swarm in compact masses of well over hundred thousand individuals remain nevertheless as enigmatic as how such a spectacular phenomenon performed by members of the second most diverse genus of animals on earth can remain so rarely observed.

KEY WORDS

Ethology; aggregation; behaviour; reproduction; hilltopping; Mediterranean Region.

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INTRODUCTION

Steninae are very distinctive slender rove beetles with broad globular compound eyes. The subfamily is distributed virtually worldwide except Antarctica and New Zealand. It consists of some 2750 extant species grouped in the genera *Dianous* Leach, 1819 and *Stenus* Latreille, 1779, the latter being the second most diverse genus of animals with approximately 2550 species (Herman, 2001; Thayer, 2005; Cai et al., 2014). Feeding essentially on collembola *Stenus* possess a chameleon-like protrusive prey-

capture mouth apparatus unique within insects, which is probably the key innovation responsible for the impressive radiation of the group (Betz, 1996, 1998). Partly because of the marked attraction of their favoured preys for humid microhabitats, Steninae are mainly found in moist forest leaf litter, near swamps, along river banks or lake shores, but also walking on the foliage of tropical rainforests. In Europe their greatest diversity is to find in moist environments such as reeds, where some species forage on humus or plants debris near the ground, while others prefer to climb on plants, or are surface

runners on bare ground (Betz, 1999a, 1999b). Although they usually possess fully functional wings, they all are very reluctant to flight, and move almost only walking or running. Hence another of their evolutionary traits appears to be a trend towards significant widening of tarsi, resulting in the apparently repeated emergence of water-gliding and swimming abilities (Betz, 2002).

In 2005 I was casually confronted to another striking peculiarity of Steninae unique within rove-beetles, which is their ability to occasionally congregate in very large numbers and form dense multilayer masses of individuals (Cuccodoro, 2007; Puthz, 2008). Submitting my few pictures and field notes to the *Stenus* specialist Volker Puthz, I was very surprised to learn that such an impressive phenomenon was still documented in the literature with only a handful of short notes since first reported some 150 years ago from France (Dufour & Perez, 1857).

Here I review the nine observations of aggregates of Steninae recorded hitherto in the literature (Dufour & Perez, 1857; Rougemont, 1980; Abdounour & Kallab, 1989; Lecoq, 1991, 1993; Cooter, 1997; Puthz, 2000; Zhao & Li, 2004; Cuccodoro, 2007), as well as sixteen additional observations reported to me by colleagues, or gathered over the internet. All the pictures available to me are presented, with some pertaining to previous records published here for the first time. The structure of these observations as well as possible causes and adaptive interests of the phenomenon are briefly discussed. Hopefully this will stimulate investigations on this phenomenon, which is definitely as spectacular as it remains enigmatic.

MATERIAL AND METHODS

Most unpublished observations were forwarded to me by Volker Puthz, Schlitz. He obtained them mainly in feedback to his repeated call for informations on the topic “*Stenus-Ansammlungen im Mittelmeerraum: wer hat solche Massenvorkommen von Stenus (Staphylinidae) auf einer kleine Fläche (unter Stein, o. ä.) beobachtet? Mitteilung Dr. V. Puthz (....)*” [*Stenus* - aggregations in the Mediterranean area: who observed such mass occurrences of *Stenus* (Staphylinidae) on a small surface (under stone, or similar)? Contact Dr. V. Puthz] published

in the rubric Von Kollege zu Kollege on the recto of the backcover of volumes 73 (1977) to 77 (1981) of the journal *Entomologische Blätter*. Several unpublished observations were also forwarded to me by the other specialists of Steninae Guillaume de Rougemont, London, and Liang Tang, Shanghai. The rest was addressed to me in feedback to my presentation on the topic at the “22nd International Meeting on Biology and Systematics of Staphylinidae” in Stuttgart (Cuccodoro, 2007) and to my call for informations addressed in June 2011 to all the email list of the announcement of 26th edition of the same meeting, or gathered by myself over the internet. When still possible I also contacted the authors of previously published reports for additional informations.

RESULTS

The observations of aggregates of Steninae are listed below organized chronologically, and consequently numbered.

1) September 1856, Saint Sever (France)

The first observation of an aggregate of Steninae was made near Saint Sever (Landes France) in the beginning of September by a local teacher named Perez (first name unknown). He brought back to Léon Dufour for identification a sample containing two thousands and several hundreds of individuals of *Stenus rusticus* Erichson, 1840 (= *Stenus picipes* Stephens, 1833), which were only a fraction of those forming the aggregate he witnessed. Curious to see the phenomenon by himself L. Dufour went there some days later with M. Perez, and they could observe it again exactly at the same place. It was on leaves of a chestnut stump cut at level with the ground located on the edge of a small, dry ravine. The leaves were completely blackened by the beetles piled one on each other. He estimated that they were more than twenty thousands individuals within an area of 50 cm in diameter. Dufour shook the leaves and heard “like a rain of sand”, so he put his hand underneath, which was readily filled with thousands of *Stenus*. These were etherized, put into a glass vial and given to his friend Joseph Alexandre Laboulbène, with charge to present that sample together with a

report of the observation at the Entomological Society of France in Paris. It was finally Léon Fairmaire, in the name of Laboulbène, who read the note of Dufour at the 22 October 1956 meeting of the Entomological Society of France (Dufour & Perez, 1857).

Note. The note is referred to as “*Stenus rusticus rencontré en immense quantité (note sur le), L. Dufour et Perez*” in the table of contents (alphabetical by taxa) at page CLXIV of tome IV of the *Annales de la Société Entomologique de France* (3rd series), in the section containing the reports the meetings of this society in the last trimester of 1856; as the last meeting reported was on 24 December 1856, it is very unlikely that the volume was published before the end of that year, hence my quotation of the reference not following Lecoq (1993), who credited the publication of the note to Fairmaire in 1856.

2) 12 June 1972, Rosas (Spain) - Figs. 1, 2

The aggregate was observed by Alfred Elbert in montains West of Rosas (Catalogna, Spain). It occurred under a large stone, and consisted of several thousands individuals of *Stenus* sp. massed in a few multilayer masses (Figs. 1, 2). Reported to V. Puthz by A. Elbert in January 1973 (V. Puthz pers. comm.).

3) 12 July 1972, Tchirtchik (Uzbekistan)

The aggregate was observed by Josef Král some 1,000-1,300 m above sea level in the Aktesch Valley near Tchirtchik in the western part of the Mts. Tienshan (Tschaktall ridge), some 50 km West of Taschkent (Uzbekistan). The Aktesh Valley is North oriented, and the place was located at base of a rocky cliff, quite humid with many stones and plants, probably occasionally flooded. Turning a 25x15 cm stone was found a 6x4 cm mass affixed to it and consisting exclusively of *Stenus* facing the edge of the stone, organized in several layers with their abdomens oriented regularly, resembling roots. Some individuals were collected using an aspirator, but as the others started to quit the mass and run away, the stone was put in a sifter in order to catch them all. No particular smell, taste, or any other inconvenience

was experienced during the process. This sample totalized 1,217 specimens of *Stenus turk* Puthz, 1972 with a sex ration of 36 females for 64 males in a random sample of 100 individuals (det. L. Hromádka). Additional masses were found under some other stones, thought only those located at a few steps of the first one, as well as in a few shadowed and wet places at base of the cliff. Reported to V. Puthz by J. Král in August 1976 (V. Puthz pers. comm.).

4) 29 September 1972, Kreta (Greece)

The aggregate was observed by Hans Malicky in the Yeropotamos river valley near the bridge below Phaistos palace (Kreta, Greece). It occurred in the late afternoon of a sunny day in a place already at shade, and consisted of more than 10,000 individuals of *Stenus picipes* (det. V. Puthz) aggregated in compact clusters hanging on a few blades of grasses near the river shore, from far looking like bee swarms. There were no stones in the area. Reported to V. Puthz by H. Malicky in August 1977 (V. Puthz pers. comm.).

5) 3 July 1977, Trimiklini (Cyprus)

The aggregate was observed by Stanislav Vit near the village of Trimiklini on the island of Cyprus. It occurred in the late morning of a sunny day on the bank of a stream in a small ravine shadowed by a gallery forest, and consisted of several thousands of *Stenus turbulentus* Bondroit, 1912 running around on only a few square meters along the steam shore, but he didn't noticed any dense multilayer masses of individuals. Reported to me by S. Vit in June 2011.

6) January 1979, Kathmandu (Nepal)

The aggregate was observed by Guillaume de Rougemont near the Dakshinkali Temple (Kathmandu, Nepal). The aggregate was estimated to consist of over 50 individuals of *Stenus immisi* Bernhauer, 1915 massed closely under a loose boulder on the bank of a stream. Frost prevailed at night. Individuals remained inactive when disturbed, apparently in state of hibernation, in sharp contrast with the activity of other specimens collec-

ted few months before in October in litter at roots of plants near a small torrent. Reported in Rougemont (1980).

7) 1981, Aurès (Algeria)

The aggregate was observed by Jean-Michel Maldas and Serge Doguet on Djebel Mamel (Aurès, Algeria). It occurred in a deep and shadowed crack of a big rock, and was estimated to consist of several thousands individuals of *Stenus cordatus* Gravenhorst, 1802. Nearby was also observed an aggregate of *Chalcoidea*. Reported in Lecoq (1993).

8) 31 August 1981, Corfu (Greece)

The aggregate was observed by Gerhard Katschak along the Ropa river on the island of Corfu (Greece). It occurred at around noon on a quite humid and 26 °C warm sunny day. In the bed of the river, which is reduced to puddled at this time of the year, were several thousands individuals of *Stenus* sp. gathered on only a few square meters close to some puddles, most quite active walking around on the ground. Sampled specimens pertained to six species: *S. hospes* Erichson 1840, *S. indifferens* Puthz, 1967, *S. pallitarsis* Stephens, 1833, *S. planifrons* Rey, 1884, *S. similis* (Herbst 1784), and *S. sinuatus* Cameron, 1930, with approximately 70% of them being *S. pallitarsis* and *S. planifrons*; sex ratio balanced. Reported to V. Puthz by G. Katschak in September and October 1981 (V. Puthz pers. comm.).

9) 27 May 1983, Tilos (Greece)

The aggregate was observed by Dieter Liebegott near the cloister of Agios Panteleimon on the island of Tilos (Greece), nearby the aggregate of *Apion* reported by Liebegott (1983). It occurred on a sunny day at noon along a small creek, and consisted of several thousands individuals of *Stenus* sp. densely grouped under some stones on a few square meters. The beetles were motionless, and massed to a depth of 2–3 bodies in the middle each group. Reported to V. Puthz by D. Liebegott in June 1983 (V. Puthz pers. comm.).

10) 27 June 1987: San Pietro Island (Italy) - Figs. 3, 4

The aggregate was observed by Maurizio Mai and Roberto Poggi at an elevation of 140 meters above sea level on the western slope of the Monte Guardia dei Mori (Fig. 3). It occurred under decaying leaves in the stony bed of a dry stream. The aggregate consisted of about 700 individuals of *Stenus* sp. intermixed with approximately an equal number of *Apion* sp., all forming one dense aggregate covering only few squares centimeters. Individuals were motionless, apparently inactive. About half of the individuals were sampled (Fig. 4), totaling 358 *Apion* (s. str.) *gracilicolle* (Gyllenhal, 1839) and 375 *Stenus* (*Parastenus*) *elegans* Rosenhauer, 1856. Reported in Lecoq (1993); additional informations and pictures sent to me by R. Poggi in July 2011.

11) June 1988, Cave Mgharet el Qlanssiyé (Lebanon) - Figs. 5, 6

The aggregate was observed by Hani Abdul-Nour, Nayla Abdul-Nour, Malaké Assouad, Fadi VBaroudi, Antoine Ghaouche, Oussama Kallab, and Paul Khawaja in the cave Mgharet el Qlanssiyé located at base of a small cliff close to a small tributary of the ouedi Qozhaïa, only few kilometres away from Kfar Sghab (Lebanon). It occurred on the ceiling of the cave at some five meters from its entrance (Fig. 5). On an area of ten square meters were some fifteen dense, black masses of *Stenus*, each several centimeters thick, with some isolated individuals walking between, for an estimated total of more than 100,000 individuals. The mass on figure 6 covered an area of about 200 cm² and was estimated to contain between 10,000 and 30,000 individuals. Amazingly some spiders were affixed with silk threads above some groups of *Stenus* sp., motionless, becoming suddenly very aggressive when approaching the hand, as if defending their larder. Specimens sampled were *Stenus cyaneus* Baudi, 1848. Reported in Abdul-Nour & Kallab (1989); original colour dia of Fig. 6 and specimens sent to me by H. Abdul-Nour in October 2007.

12) July 1988, Pyrénées orientales (France)

The aggregate was observed by Jean-Claude

Lecoq at some 1200 m above sea level close to the top of Pic Néoulou (Pyrénées orientales, France). It occurred under a 30x40 isolated stone lying on wet grass close to the tree line, and consisted of several thousands individuals densely grouped on an area large as two hands. Individuals were nearly motionless. Specimens sampled were *Stenus cordatus*; sex ration balanced. According to his experience the species is not very common in the area, and individuals were kilometers away of their nearest favorite habitat. Reported in Lecoq (1991).

13) 1994, Sichuan (China)

The aggregate was observed by Fa-Ke Zheng on the Emeishan in Sichuan (China), and consisted of several thousands *Dianous freyi* Benick, 1940 gathered in dense multilayer masses on and under a large boulder near a stream. Reported in Puthz (2000).

14) May 1996, Zhejiang (China)

The aggregate was observed by John Cooter in the Long Wang Shan Nature Reserve (Zhejiang, China), and consisted of several thousands *Dianous freyi* in a deep horizontal crevice under a huge boulder resting on bare rock on the bank of a stream. They were near motionless in the deep shade, forming a continuous mass 1–2 cm deep and 3–5 cm across, and extending for well over one meter. Nearby specimens of *D. banghaasi* Bernhauer, 1916 were active at the sun on the bare rock, while individuals of *D. freyi* would actively seek shelter in shallow crevice or under dead leaves when disturbed. Reported in Cooter (1997).

15) 2 June 1999, Sardegna (Italy)

The aggregate was observed by Roberto Poggi at some 1000 meters above sea level nearby Genna Silana at Fonte Esilai (Sardegna, Italy). It occurred near a stream, and consisted of several hundreds individuals of *Stenus* sp. very densely grouped together. Specimens sampled pertained to two species: *S. cordatus* and *S. elegans*. Reported to me by R. Poggi in July 2011.

16) 16 August 2000, Guangdong (China) - Figs. 7, 8

The aggregate was observed by Graham T. Reels in the Chebaling Nature Reserve (Guangdong, China). It occurred by a stream in subtropical forest, and consisted of several thousands *Dianous* sp. densely massed in four separate groups near the base of a single very large boulder (Fig. 7). All the beetles were motionless, and massed to a depth of 4–5 bodies in each group (Fig. 8). A sample from two of the masses made by scooping an open tube through the beetles included about 250 individuals of *D. banghaasi*, and a single individual of an undescribed species. Reported to G. de Rougemont by G.T. Reels in September 2000 (G. de Rougemont pers. comm.).

17) May 2003, Zhejiang (China)

The aggregate was observed by Liang Tang and Li-Zhen Li some 300 meters above sea level on Mt. Tianmushan (Zhejiang, China). It occurred during a cloudy day on the boulders of a big stream, and consisted of several hundreds *D. banghaasi* and *D. freyi* densely grouped on each other on a few square centimeters close to the water surface. Reported with a picture in Zhao & Li (2004); additional information reported to me by L. Tang in June 2011.

18) 25 July 2003, Guizhou (China)

The aggregate was observed by Liang Tang at 700 meters above sea level on Mt. Fanjingshan (Guizhou, China). It occurred during a sunny day on a boulder in a big stream, and consisted of about hundred *Dianous* sp. pertaining to two distinct species with red elytral spots, individuals densely grouped on each other on a few square centimeters. Reported to me by L. Tang in June 2011.

19) 2004, Nanchong (China)

The aggregate was observed by Fa-Ke Zheng in Nanchong (China). It occurred on a boulder close to a stream, and consisted of large numbers of *D. banghaasi* (not *D. freyi*, G. de Rougemont pers. comm.) on a very small area. Reported in Zhao & Li (2004).

20) 17 and 19 October 2005, Mt Barail (India) - Figs. 9–15

The aggregate was observed by Alessandro Marletta and me near the town of Haflong (North Cachar Hills) in the cloud forest located at the top of the 1800 m high Mt. Barail (Assam, India) (Fig. 10). It occurred at the edge of the summital clearing (Fig. 9), and consisted of more than five thousands individuals densely concentrated at base of a small tree.

We discovered the aggregate in the early afternoon of a rather cloudy day. Individuals were almost everywhere up to 1.5 m high on the mossy stem (Fig. 11), as well scattered at a few centimeters from each other almost everywhere over the surrounding couple of square meters of vegetation (Fig. 13, 14). Density of individuals was particularly high underneath some recurved dead broadleaves and in shallow cavities of thin dead branches, where they formed compact multilayer masses (Fig. 12). Most individuals appeared moderately active, with many couples *in copula* (Fig. 14). Specimens sampled were all *Stenus stigmatias* Puthz, 2008; sex ration balanced. The aggregate was still going on when we left the place at 3.30 PM. The following morning we returned there and settled our camp for further investigations, but couldn't find even a single *Stenus*, and rain started pooring on us from 3 PM until late in the night. The day after was sunny until clouds obscured the sun from late morning throughout the afternoon. At about 1 PM we suddenly noticed again some *Stenus* near the same particular tree. As if they were oosing out of its trunk and basal branches (Fig. 12), their number increased dramatically and within half an hour the aggregate had resumed with the same intensity as two days before. At around 4 PM, the attendants at the aggregate appeared to have significantly decreased in number, and they were all gone before sunset a 4h30 PM. I returned and camped there at the same period of the year during two weeks in 2006 and one week in 2008, but couldn't see again even one individual of *S. stigmatias*. Reported in Cuccodoro (2007) and Puthz (2008).

21) September–November 2005–2009, Montefiascone (Italy) - Figs. 15–19

The aggregate was observed by Anonymous in

the village of Montefiascone, located on a small rocky hill two kilometers away from the eastern shore of lake Bolsena (Latium, Italy) (Fig. 15). It occurred inside a refurbished part of a very ancient house and its underground cellar (Fig. 16, 17), both adjoining to the thousand years old castel erected on top of that 620 m high local summit. Consisting of more than hundred thousands individuals, the phenomom lasted several weeks typically from late September to late November, and reoccurred annually at least from 2005 to 2008. It was so intrusive that the owner of the house and his family moved out during that period of the year. Despite intensive efforts to seal every possible entrance into the house (mosquito nets at windows, joining around the door and windows frames, etc.) the owner never succeeded to prevent the *Stenus* sp. from coming, and then going out. He never saw them flying. Amazingly individuals tended to concentrate in dark places (angles of the rooms, under the furnitures, etc., Fig. 18), but they were moving rather toward the windows while aggregated. During these seasonal invasions individuals were seen mating (Fig. 19), and only very few dead specimens were left behind after leaving. The phenomom never occurred elsewhere in the neighborhood, and stopped after heavy sanitation works were carried out in and around the house in Spring 2009. Reported on the WEB (Forum Entomologi Italiani) by Anonymous in March 2009; further informations reported to me by Anonymous in March 2009.

22) June 2009, Hainan Island (China)

The aggregate was observed by Anonymous in Yingeling Nature Reserve (Hainan Island China). It occurred on leaf litter in forest near the mountain summit, and consisted of several thousands *Stenus* sp. pertaining to at least two species (one black with red spots and the other bluish black) intermixed on a very small area. Reported to me by L. Tang in June 2011.

23) 9 September 2010, Komirshi river (Kazakhstan) - Figs. 20–23

The aggregate was observed by Vitaly Katscheev in the gorge of river Komirshi (Kyrgyz Alatau, Kazakhstan, Fig. 20), and consisted of more than four hundred individuals of *Stenus turk* form-

ing a continuous congestion on a 20x30 cm platform under a willow bush close to a stream (Figs. 21–23). Only individual specimens were found nearby, with an average density of 18.7 individuals per square meter on the 10 square meters around this bush. Reported to V. Puthz by V. Katscheev in January 2011 (V. Puthz pers. comm.).

24) 13 May 2011, Mt. San Angelo (Italy)

The aggregate was observed by Pavel Krásenský at an elevation of 815 m above sea level on the North slope of Mt. Saint Angelo (Apulia, Italy) during a sunny day with about 15 °C at shadow, and no wind. It occurred near the entrance of a small cave located - 41°42'36.1"N 15°56'33.8"E - in a sheltered depression in oak forest, and consisted of about 200 to 300 *Stenus cordatus* scattered on the grass on an area of about ten square meters completely at shade. The specimens quickly ran on the grass, and about half of them flown. After about 15 minutes of observation the specimens slowly disappeared. Reported to me by P. Krásenský in February 2016.

25) 22 November 2014, Virajpet (India) - Figs. 24–28

The aggregate was observed by Vipin Baliga and A.K. Karthik near Virajpet (Karnataka, India). It occurred in a sheltered depression on the vertical face of a huge boulder adjacent to a stream, and consisted of several thousands of *Stenus* sp. grouped in two dense masses (Figs. 24, 25). As they were taking pictures, they noticed that individuals were slowly dispersing, moving away from the groups (Figs. 26–28). After a few pictures they went ahead and while returning found them scattered over a greater area. Despite my efforts I couldn't spot a couple *in copula* in the close up pictures of the aggregate (Figs. 26, 27). Reported on the WEB (India Biodiversity Portal) by V. Baliga in December 2014; further informations reported to me by V. Baliga in February 2017.

26) 5 February 2015, Agumbe (India) - Figs. 29–33

The aggregate was observed by Lukáš Podloucký at some 100 meters above sea level near the Onake Abbi falls at Agumbe (Karnataka, India). It

occurred at around 2 PM of a 30-35 °C hot sunny day on the stem of tree shaded by branches close to a stream (Fig. 29). Estimated to consist of more than hundred thousand individuals densely grouped in one multilayer mass it is by far the largest *Stenus* aggregate ever photographed (Figs. 30-33). The mass did not change shape, nor moved during the quarter of an hour it was surveyed. Only after small disturbance (blow, touch, ...) some individuals tried to escape from the shape of the mass, and some of the tree. Despite my efforts I couldn't spot a couple *in copula* in the close up pictures of the aggregate (Figs. 32, 33). Reported on the WEB (Friends of Coleoptera Entomology department Facebook page) by J. Kadlec in December 2015; further informations reported to me by L. Podloucký in December 2015.

DISCUSSION AND CONCLUSIONS

This collection is very heterogeneous, and at first glance quite puzzling. It seems in fact that this assemblage deals with different kinds of phenomena, with some of them probably even mixed up. So at this level of knowledge (rather of ignorance) it would be certainly very hazardous to draw any definitive interpretation to most of them. However some considerations can nevertheless be made.

First both the genera *Dianous* and *Stenus* are involved. And some species are more frequently cited, notably *S. cordatus* (reports 1, 12, 15 and 24), *S. elegans* (reports 10 and 15), and *S. turk* (reports 3 and 23), and *D. banghaasi* (reports 16, 17 and 19) and *D. freyi* (reports 13, 14, 17). More frequent aggregative behaviour in these taxa might reflect either a higher sensibility to drought of these two *Dianous* species inhabiting in subtropical climate, or in the contrary a better adaptation precisely to long periods of draught of these three *Stenus* species inhabiting in the Mediterranean climate.

However considering the megadiversity and ubiquity of the subfamily, in particular of the genus *Stenus*, and in the light of the repeated calls for observations on the topic made since 1977 it is quite astonishing that the new total of reports since 1856 is of twenty six only. Many staphylinists who

spent years of their life in cumulate fieldwork throughout the world never had the chance to witness a *Stenus* aggregate. And for the few lucky ones it mostly remained a once in a lifetime experience to which they were unprepared, hence the scarcity of the pictures made. Fortunately the phenomenon is truly so impressive that it stroke the attention even of non-specialists, to whom we owe the best and most impressive pictures available (Figs. 24–33). This indicates clearly that even if possibly common in some stenine taxa, aggregative behaviour certainly remains very exceptional within the subfamily.

Generally speaking it is not so uncommon to find Steninae concentrated in high population density in some peculiar suitable biotopes. For example sometimes hundreds, or even thousands individuals of *Stenus* may inhabit mossy spots over rocky slope, and assemblages of several species of *Dianous* can also rather frequently be seen by dozens feeding at base of some particular boulders in streams. Nevertheless those specimens are always separated one from another with some distance, doing their own business apparently without communicating with each other. This could well be the case for the reports 5 and 8, the later consisting of a congregation of six different species of *Stenus*.

Several observations seem also to refer to individuals grouped together in a common attempt at minimizing negative abiotic factors, such as high or low temperature, or low humidity. These groups would hence be formed by individuals gathering together in most suitable microhabitats of their environment, like under stones (for humidity, and heat or cold), or in caves (for humidity and cold), with individuals remaining rather inactive, not necessarily engaged in elaborate interactions between each other, like mating. Such behaviour would be expected to occur rather on circadian and/or seasonal basis. For example all the reports pertaining to *Dianous* sp. were consistently made in subtropical climate with individuals grouped on boulders close to streams (reports 13, 14, 16–19; Figs. 7, 8); insects could seek there fresh and humid during the hottest hours of the day, but still remaining close enough to their normal habitat in order to be able to readily return there once the ambient conditions will be back to their liking. As

already noted by Rougemont (1980) it is also very likely that the small group of *S. immisi* he found in January in Nepal massed together and inactive were individuals hibernating during excessive cold (report 6). Same could apply to the aggregate observed in January in Khazakstan (report 23). Similarly most observations from the Mediterranean area (reports 1, 7, 9, 10, 11, 15 and 24) and that from Uzbekistan (report 3; Figs. 20–23) might refer to populations of *Stenus* in state aestivation trying to escape excessive drought under stones, or in caves. Particularly impressing is that aggregate observed in Lebanon inside the “rove beetles cave” (report 11), where the masses of *Stenus* were “guarded” by spiders (Fig. 6).

Considering the rather individualistic normal behaviour of these insects, it seems obvious that pheromone signals drive them to form such dense masses consisting of several layer of bodies tightly piled onto each other. However the reasons which would trigger those pheromones signals remain very obscure. The most seducing hypothesis is that aggregative behaviour would facilitate reproduction, and hence those signals would be triggered on seasonal basis. This would be particularly tempting to explain when *Stenus* are surprized in compact clusters grouped above the ground on leaves of a tree (report 1), hanging on a few blades of grasses (report 4), or forming very compact masses in full view on a boulder (report 25; Figs. 24–28) or a tree (report 26; Figs. 29–33). However at least for these last two reports (25 and 26), which were those documented with the best pictures ever of the phenomenon, it seems that there were no specimens mating (see Figs. 26, 27, 32, 33). So far the only evidences of specimens *in copula* during or after an aggregation pertain to observations made in India (report 20; Fig. 14) and in Italy (report 21; Fig. 19).

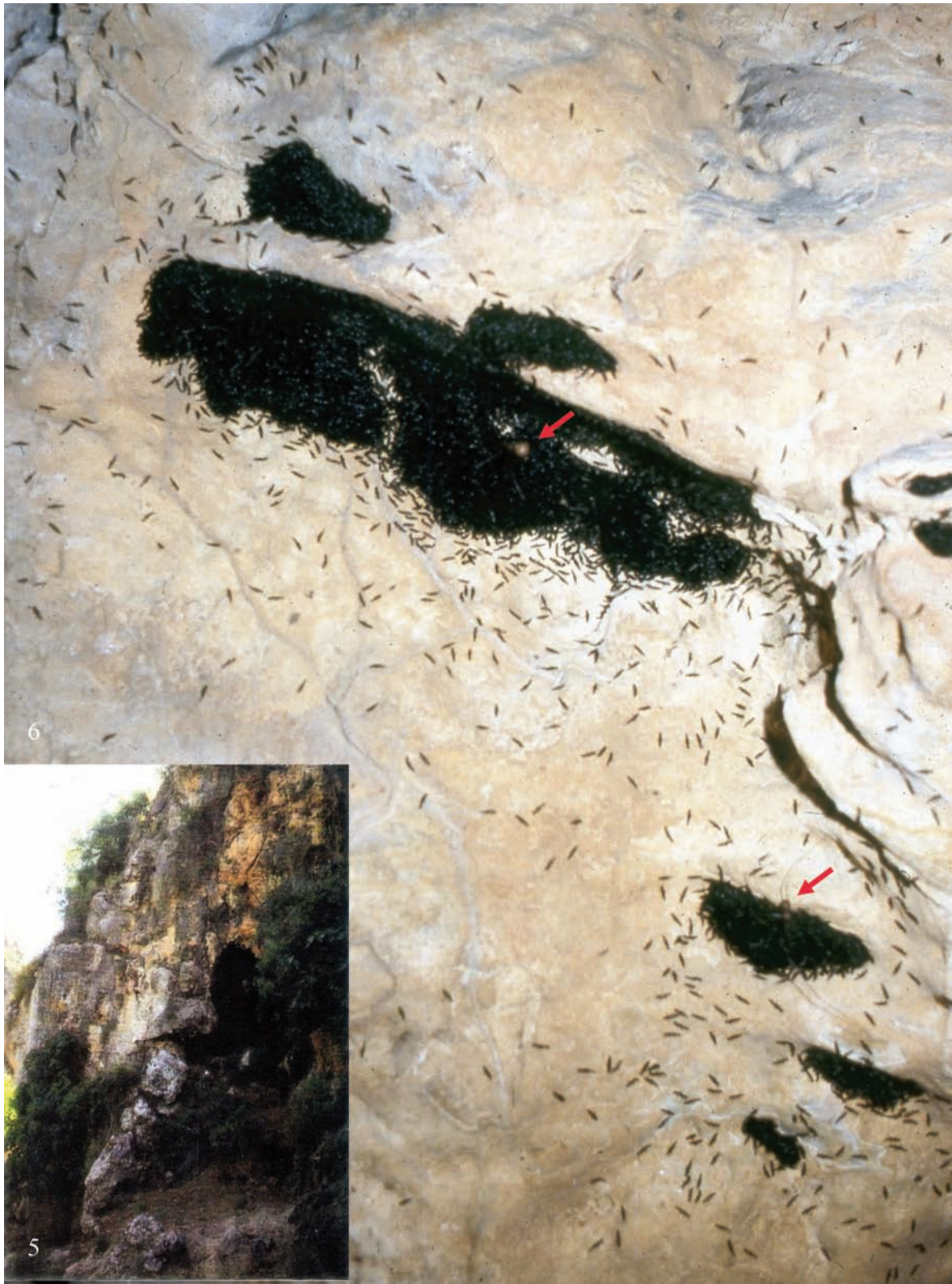
The two latter reports (20 and 21) together with report 1 are amazingly also the only three aggregates having reoccurred at least two times at the same place: on a particular tree at several days of interval for reports 1 and 20, and inside a house and its cellar over several years for report 21. Recurrence of an aggregate on a very precise location is also very hard to explain without the implication of lasting pheromone signals.



Figures 1, 2. Aggregate n° 2 (12.VI.1972: Rosas, Spain, credit A. Elbert). Views of the stone with dense multilayer masses of *Stenus* sp. (black masses), and isolated individuals walking away.



Figures 3, 4. Aggregate n° 7 (27.VI.1987: San Pietro Island, Italy, credit R. Poggi). View of the biotope and sample of the aggregate, with sifter and sheet covered with many individuals of *Stenus* (red arrow showing one) and *Apion* (blue arrow showing one) running out of the sifter and on the sheet.



Figures 5, 6. Aggregate n°11 (June 1988: Cave Mgharet el Qlanssiyé, Lebanon, credit H. Abdul-Nour). Entrance of the cave and dense multilayer masses of *Stenus cyaneus*, the main one covering about 200 cm², with their « guardian spider » (red arrows).



Figures 7, 8. Aggregate n°16 (16.VIII.2000, Guangdong, China, credit G.T. Reels). Fig. 7: boulder with several thousands *Diadous banghaasi* (dark areas) densely massed in four separate groups near the base. Fig. 8: close up of upper group with individuals massed in 4 to 5 layer.



Figures 9, 10. Aggregate n° 20 (17 and 19.X.2005: Mt Barail, India, credit G. Cuccodoro). Fig. 9: view of the biotope (red arrow showing the location of the aggregate). Fig. 10: view of the western slope of Mt Barail (red arrow showing the location of the aggregate) from Haflong (North Cachar Hills, Assam).



Figures 11, 12. Aggregate n° 20 (17 and 19.X.2005: Mt Barail, India, credit G. Cuccodoro). Fig. 11: mossy stem of the tree where the aggregate was observed twice at two day of interval thousands (red arrow showing the branch photographed in figure 12). Fig. 12: densely massed *Stenus stigmatias* as if oozing out of a dead branche.



Figures 13, 14. Aggregate n° 20 (17 and 19.X.2005: Mt Barail, India, credit G. Cuccodoro). Figs. 13, 14: *Stenus stigmatias* over the vegetation near the tree of figure 11 (red arrows showing couples *in copula*).



Figures 15–19. Aggregate n° 21 (September–November 2005–2008, Montefiascone, Italy, credit Anonymous, WEB (Forum Entomologi Italiani) in March 2009). Fig. 15: view of the Lake Bolsena from the site of the aggregate. Fig. 16: view of the biotope, with cellar. Fig. 17: entrance of the cellar inside which part of the aggregate occurred repeatedly in Autumn over several years (red arrows showing area with *Stenus*). Fig. 18: multilayer mass of *Stenus* sp. in the corner of a room inside the house. Fig. 19: *Stenus* sp. walking out of the cellar shown in figure 17 (red arrows showing couples in copula).



Figures 20–23. Aggregate n° 23 (15.XII.2010, Komirshi river, Kazakhstan, credit V. Katscheev). Fig. 20: view of the biotope. Figs. 21, 22: views of the microhabitat (red arrow showing the location of the aggregate). Fig. 23: sifter with hundreds *Stenus turk* running away.



Figures 24–28. Aggregate n° 25 (22.XI.2014, Virajpet, India, credit V. Baliga). Figs. 24, 25: Views of the entire *Stenus* sp. aggregate. Figs. 26, 27: details of the aggregate (note the apparent absence of couples in copula). Fig. 28: close up of three *Stenus* sp. walking away of the aggregate.



Figures 29–33. Aggregate n° 26 (5.II.2015, Agumbe, India, credit L. Podloucký). Fig. 29: view of the biotope (red arrow showing the location of the aggregate). Fig. 30: view of the main part of the aggregate. Fig. 31: close up of the central part of the aggregate. Figs. 32, 33: close ups of the lower part of the aggregate (note the apparent absence of couples in copula).

Aggregate	Year	Country	Climate	Month	Species involved	Exposure	Multilayer	Stream	Hilltop	Matings	Pictures
1	1856	France	Cool temperate	September	<i>Stenus cordatus</i>	in full view	yes	no			
2	1972	Spain	Mediterranean	January	<i>Stenus</i> sp.	hidded	yes				Figs. 1, 2
3	1972	Uzbekistan	Warm continental	July	<i>Stenus turk</i>	hidden	yes	yes			
4	1972	Greece	Mediterranean	September	<i>Stenus picipes</i>	in full view	yes	yes			
5	1977	Cyprus	Mediterranean	July	<i>Stenus</i> sp.	in full view	no	yes			
6	1979	Nepal	Subtropical	February	<i>Stenus immsi</i>	hidden	no	yes			
7	1981	Algeria	Cold semiarid		<i>Stenus</i> sp.	hidden	yes				
8	1981	Greece	Mediterranean	August	<i>Stenus</i> (6 sp.)	in full view	no	yes			
9	1983	Greece	Mediterranean	May	<i>Stenus</i> sp.	hidden	yes	yes			
10	1987	Italy	Mediterranean	June	<i>Stenus elegans</i> + <i>Apion</i> sp.	hidded	yes	yes			Figs. 3, 4
11	1988	Lebanon	Mediterranean	June	<i>Stenus cyaneus</i>	hidden	yes	yes			Figs. 5, 6
12	1988	France	Cool temperate	July	<i>Stenus cordatus</i>	hidden	yes	no	yes		
13	1994	China	Subtropical		<i>Dianous freyi</i>	in full view	yes	yes			Puthz,2000
14	1996	China	Subtropical	May	<i>Dianous freyi</i>	hidden	yes	yes			
15	1999	Italy	Mediterranean	June	<i>Stenus elegans</i> + <i>Stenus cordatus</i>	in full view		yes			
16	2000	China	Subtropical	August	<i>Dianous banghaasi</i> + <i>Dianous</i> sp.	in full view	yes	yes			Figs. 7, 8
17	2003	China	Subtropical	May	<i>Dianous banghaasi</i> + <i>Dianous freyi</i>	in full view	yes	yes			Zhao & Li, 2004
18	2003	China	Subtropical	July	<i>Dianous</i> sp (2 sp.)	exposed	yes	yes			
19	2004	China	Subtropical		<i>Dianous banhaasi</i>	exposed	yes	yes			
20	2005	India	Subtropical	October	<i>Stenus stigmatias</i>	in full view	yes	no	yes	yes	Figs. 9-14
21	2005- 2008	Italy	Mediterranean	September- November	<i>Stenus</i> sp.	hidden	yes	no	yes	yes	Figs. 15-19
22	2009	China	Subtropical	June	<i>Stenus</i> sp. (2 sp.)	in full view		no	yes		
23	2010	Kazakhstan	Warm continental	December	<i>Stenus turk</i>	hidden	yes	yes			Figs. 20-23
24	2011	Italy	Mediterranean	May	<i>Stenus cordatus</i>	in full view	no				
25	2014	India	Tropical	November	<i>Stenus</i> sp.	in full view	yes	yes		no	Figs. 24-28
26	2015	India	Tropical	February	<i>Stenus</i> sp.	in full view	yes	yes		no	Figs. 29-33

Table 1. Summary of the 26 observations of aggregates of Steninae reported since 1856 (Coleoptera Staphylinidae).

Together with the reports 12 (from France) and 22 (from China) these same two reports (20 and 21) belong even more amazingly to the four aggregates of *Stenus* found near or at the top of a local summit, with specimens over one kilometer away from their usual habitat, corroborating the suggestion by Lecoq (1991) of a possible hilltopping effect on the phenomenon. Although *Steninae* can fly (see report 24), they are basically very lousy flyers and prefer walking. On the top of Mt. Barail I have not seen even one specimen flying to or away of the two consecutive aggregates I watched there for over 6 cumulated hours (report 20). But the key advantage for their survival these one centimeter long rove beetles would find in walking at least half a kilometer away of their habitat up to the top of this 1800 m high summit is quite obscure to me.

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