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Experimental crossing of *Carabus (Damaster) fruhstorferi* Roeschke, 1900, with different subspecies of *Carabus (Coptolabrus) smaragdinus* Fischer, 1823, yielding fertile F1 hybrids (Coleoptera, Carabidae)

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Résumé

Le croisement de *Carabus (Damaster) fruhstorferi* Roeschke, 1900, endémique de l'île Tsushima de l'archipel japonais avec différentes sous-espèces de *Carabus (Coptolabrus) smaragdinus* Fischer, 1823, de Corée et de Chine apporte des hybrides de première génération avec une bonne prolificité. De façon très inattendue, certains de ces hybrides de première génération sont interféconds. Le niveau de fécondité est néanmoins dépendant de la sous-espèce de *Carabus (Coptolabrus) smaragdinus* Fischer, 1823, parente. Ces résultats sont à rapprocher de ceux observés lors des croisements de *C. (Coptolabrus) lafossei dabieshanus* Imura, 1996, avec *C. (Coptolabrus) nankotaizanus* Kanô, 1932, ainsi qu'avec *C. (Damaster) frushtorferi* Roesche, 1900.

Abstract

The crossing of *Carabus (Damaster) fruhstorferi* Roeschke, 1900, endemic to the island of Tsushima of the Japanese archipelago with different subspecies of *Carabus*

(Coptolabrus) smaragdinus Fischer, 1823, from Korea and China brings first generation hybrids with good prolificity. Some of these first generation hybrids are interfertile in an unexpected way. The level of fertility is nevertheless dependent on the parent subspecies of *Carabus (Coptolabrus) smaragdinus* Fischer, 1823. These results are reminiscent of those observed during the crossing of *C. (Coptolabrus) lafossei dabieshanus* Imura, 1996, with *C. (Coptolabrus) nankotaizanus* Kanô, 1932, and with *C. (Damaster) fruhstorferi* Roesche, 1900, too.

Keywords

Coleoptera, Carabidae, *Carabus*, *Coptolabrus*, *Damaster*, hybridization, China, Japan, Korea.

The taxonomy of the genus *Carabus* is in constant evolution as evidenced by the important review works carried out by T. Deuve (2021). It is now clear that the contributions of molecular biology studies both at the level of the nuclear genome (Sota *et al.*, 2004; Deuve, 2012; Deuve *et al.*, 2012) and the mitochondrial genome (Osawa *et al.*, 2004) allow a clarification of the relationships of the different subgenera and species between them, even if important gaps or difficulties of interpretation remain as shown by the recent modifications made by T. Deuve in his most recent classification (Deuve, 2025).

A complementary approach to better understand their relationships is to study the species *in vivo* in order to get more data on their genetic proximity, thanks to the experimental hybridization results. This is the aim of many authors who continue to study the possibility of breeding and interspecific or even intersubgeneric experimental crossing experiments in order to better identify the genetic relationships of the species of the genus *Carabus* (Busato *et al.*, 2014; Dubois *et al.*, 2022; Godeau *et al.*, 2007; Sapaly *et al.*, 2013).

We have been engaged in such crossing experiments for more than 15 years and obtained a lot of F1 hybrids derived from *Coptolabrus, Damaster* and *Acoptolabrus* species showing a genetic proximity of the species studied (Dubois, 2015). But we recently published new results dealing with F1 hybrids which prove to be interfertile showing, in this case, an extremely close genetic proximity. Our experimental crossbreeding of species of the *Coptolabrus* subgenus led to the discovery of interfertile F1 hybrids. We observed that hybrids obtained by crossing *C. (Coptolabrus) lafossei dabieshanus* with *C. (Coptolabrus) nankotaizanus* were interfertile over two generations (Dubois, 2013). Similarly, we then obtained new results by crossing *C. (Coptolabrus) lafossei dabieshanus* Imura, 1996, with *C. (Damaster) fruhstorferi* Roeschke, 1900 (Dubois *et al.,* 2022) leading to interfertile F1 hybrids.

Continuing our efforts to identify new closely related species, among numerous interspecific hybrids of *C. Coptolabrus* crosses with different Asian *Coptolabrus* and *Damaster* species which generally prove to be sterile, we found that the subspecies *C. (Coptolabrus) smaragdinus euviridis* Ishikawa et Kim, 1983, crossed with *C. (Damaster) fruhstorferi* Roeschke, 1900, gave F1 hybrids that are interfertile giving F2 hybrids. This unexpected discovery, which did not involve *C. (Coptolabrus) lafossei dabieshanus* Imura, 1996, led us to investigate furthermore the relationship between these two species. Therefore, we crossed *C. (Damaster) fruhstorferi* Roeschke, 1900, with four other different subspecies of *C. (Coptolabrus) smaragdinus* Fischer, 1823, in order to better understand the genetic relationship that might exist between these two species. In particular, we wanted to know if this genetic proximity was modulated when different populations of *C. (Coptolabrus) smaragdinus* Fischer, 1823, were involved in the crossings with *C. (Damaster) fruhstorferi* Roeschke, 1900, which is endemic to Tsushima Island.

Material and method. – Breeding and hybridization experiments were conducted under the now well-established conditions (Malausa, 1977) which proved appropriate for the species *C. (D.) fruhstorferi* and *C. (C.) smaragdinus*. For all the experiments, we collected eggs in order to get data about the fecundity of females. It is important then to isolate the first stage (L1) larvae as soon as they appear in order to avoid any risk of cannibalism. To facilitate the reading of this paper, we shortened the names of the different taxa and hybrids using abbreviations mentioned above in bold. Specimens of every species and subspecies involved in this study are shown in Fig. 1-6.

Locations of the collected genitors are:

C. (D) fruhstorferi Roeschke, 1900, (**Fsh**) were collected from Tsushima Island (Japan)
C. (C) smaragdinus monilifer Tatum, 1847, (**Smm**) were collected from Seogwipo-si, Jeju Island, South Korea
C. (C) smaragdinus euviridis Ishikawa et Kim, 1983, (**Sme**) were collected from Gyeongsangnam-do, Sancheong-gun, Sicheon-myeon, South Korea
C. (C) smaragdinus branickii Taczanowski, 1887, (**Smb**) were collected from Nae-myeon, Hongcheon-gun, Gangwon Province, South Korea
C. (C) smaragdinus furumiellus Deuve, 1994, (**Smf**) were collected from Liaoning province, China
C. (C) smaragdinus honanensis Hauser, 1921, (**Smh**) likely collected from Henan province, China

Experimental results

For a good understanding of the text, we always mention the name of hybrid individuals starting with the name of the species of the female(s) used for the crossing followed by the name of the species of the male(s) used.

We cannot describe in details the numerous experiments carried out, so we will give the data of each types of crossing using tables.

The crossing experiments require virgin individuals, so we first made strains of every taxa used. For each type of crossing, depending of the available individuals, we made either only one experiment in breeding boxes containing one or two couples of genitors, or we made separated experiments in several boxes. The numbers mentioned in the tables are the total number of females and males involved in a given crossing type and the corresponding pooled data.

Crossings leading to F1 hybrids

Table 1 indicates in the first column the obtained F1 hybrids, then the total number of parent females and males involved, the number of eggs collected, the stage one larvae (L1) obtained, the number of well-formed F1 hybrid imagines, the fecundity of the parent female, measured as the number of eggs divided by the number of females, the prolificity defined as the ratio of imagos/ L1, the ratio F1 imagines/eggs which can be considered as a measure of the fecundity of the parent males.

F1	♀	♂	eggs	L1	imagines	fecundity	prolificity	imagines/eggs
FshSmm	4	2	117	96	75(38F 37M)	29.25	0.78	0.64
SmmFsh	1	2	16	15	11(5F 6M)	16	0.73	0.68
FshSme	6	3	119	54	27 (18F 9M)	19.83	0.50	0.23
SmeFsh	2	4	33	26	18 (9F 9M)	16.5	0.69	0.54
FshSmb	4	2	61	41	29 (19F 10M)	15.25	0.70	0.47
SmbFsh*	1	2	9	3	3 (2F 1M)	9.0	1.0	0.33
FshSmf	5	3	83	57	38 (23F 15M)	16.6	0.66	0.45
FshSmh	6	3	111	33	19 (5F 14M)	18.5	0.57	0.17
SmhFsh	6	4	26	21	13 (7F 6M)	4.3	0.61	0.50

Table 1: Data obtained for F1 hybrids (* These data are not significant due to contamination of the genitors with mites. This affected both the genitors and the collected eggs. The female died prematurely).

As shown in Table 1, we performed all the possible crossings with the available taxa. We made each crossing in both directions because it has been published several examples of hybridization experiments showing an asymmetric male fertility (see discussion). However, all crossings performed in this study gave larvae and F1 hybrid imagines. The obtained imagines are well formed and

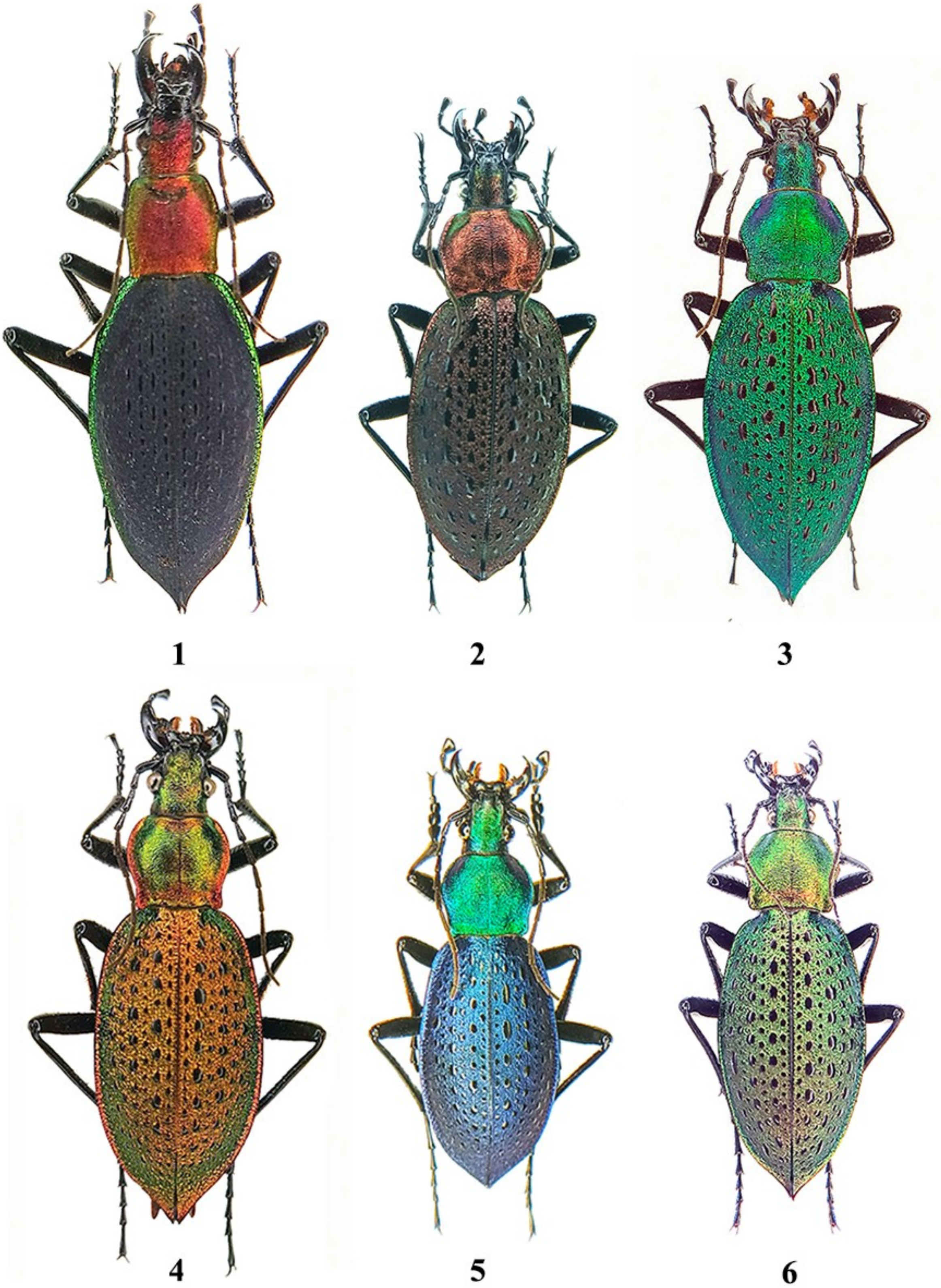

Fig. 1-6 : *C. (Coptolabrus)* and *C. (Damaster)* taxa involved in the crossings. – 1, ♀ *C. (D.) fruhstorferi* Roeschke, 1900.– 2, ♀ *C. (C.) smaragdinus monilifer* Tatum, 1847. – 3, ♀ *C. (C.) smaragdinus euviridis* Ishikawa & Kim, 1983. – 4, ♀ *C. (C.) smaragdinus branickii* Taczanowski, 1887. – 5, ♂ *C. (C.) smaragdinus furumiellus* Deuve, 1994. – 6, ♀ *C. (C.) smaragdinus honanensis* Hauser.

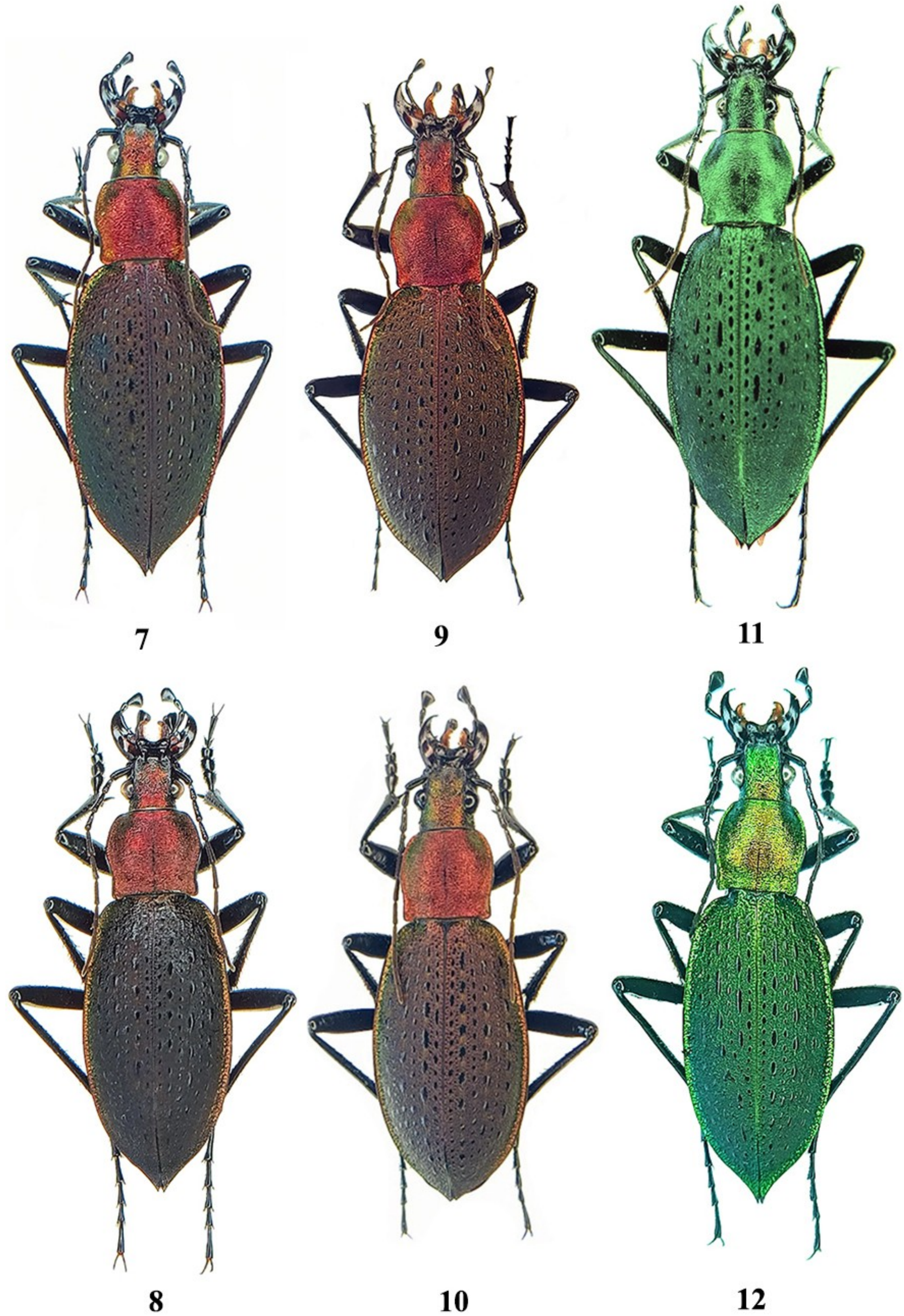

Fig. 7-12 : F1 hybrids. – 7, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus monilifer*). – 8, ♂ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus monilifer*). – 9, ♀ (♀ *C. (C.) smaragdinus monilifer* X ♂ *C. (D.) fruhstorferi*). – 10, ♂ (♀ *C. (C.) smaragdinus monilifer* X ♂ *C. (D.) fruhstorferi*). – 11, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus euviridis*). – 12, ♂ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus euviridis*).

healthy. After feeding for 4 to 6 weeks at room temperature, they become sexually mature. We did not observe significant differences for the duration of the development during all these experiments. The temperature is the main factor of variation. For example, at 26-28 °C, the full development starting from a collected egg has been only about 30 days. This very short development time allows us to investigate, in some cases, the putative fertility of the F1 hybrids by intercrossing them during the same year.

Fig. 7-12 and 13-18 show representative examples of F1 hybrid females and males obtained.

Crossings leading to F2 hybrids

Similarly to the previous experiments, Table 2 shows as in Table 1, the obtained data.

F2	♀	♂	eggs	L1	imagines	fecundity	prolificity	imagines/eggs
FshSmm	21	22	79	66	41 (20F 21M)	3.76	0.62	0.51
SmmFsh	4	4	82	55	32 (12F 20M)	20.5	0.58	0.39
FshSme	14	7	44	18	9 (5F 4M)	3.1	0.5	0.20
SmeFsh	8	9	60	27	12 (6F 6M)	7.5	0.44	0.20
FshSmb	9	9	94	80	34 (17F 17M)	10.44	0.42	0.36
SmbFsh*	2	1	13	7	1 (1F)	6.5	0.14	0.07
FshSmf	11	12	117	6	2 (1F 1M)	10.63	0.05	0.017
FshSmh**	4	7	6+x	0	0	1.5 (> ?)	0	0
SmhFsh	4	7	31	0	0	7.75	0	0

Table 2: Data obtained for F2 hybrids (* These data are not significant due to contamination of the genitors with mites; this affected both the genitors and the collected eggs. ** The eggs were not collected in our first crossing trial).

Figures 19-24 show some examples of the F2 hybrids. As we previously observed for second generation hybrids, the phenotypes of the imagines are more diverse. In particular, the differences in colors are more pronounced than for F1 hybrids. For example, some F2 hybrids derived from *C. (C.) smaragdinus branickii* show a green color instead of the bronze or copper color induced by *C. (C.) smaragdinus branickii* parents (see Fig. 6).

However, a clear decrease of fertility seems to occur with F1 hybrids derived from the subspecies *C. (C.) smaragdinus furumiellus*. For F1 hybrids

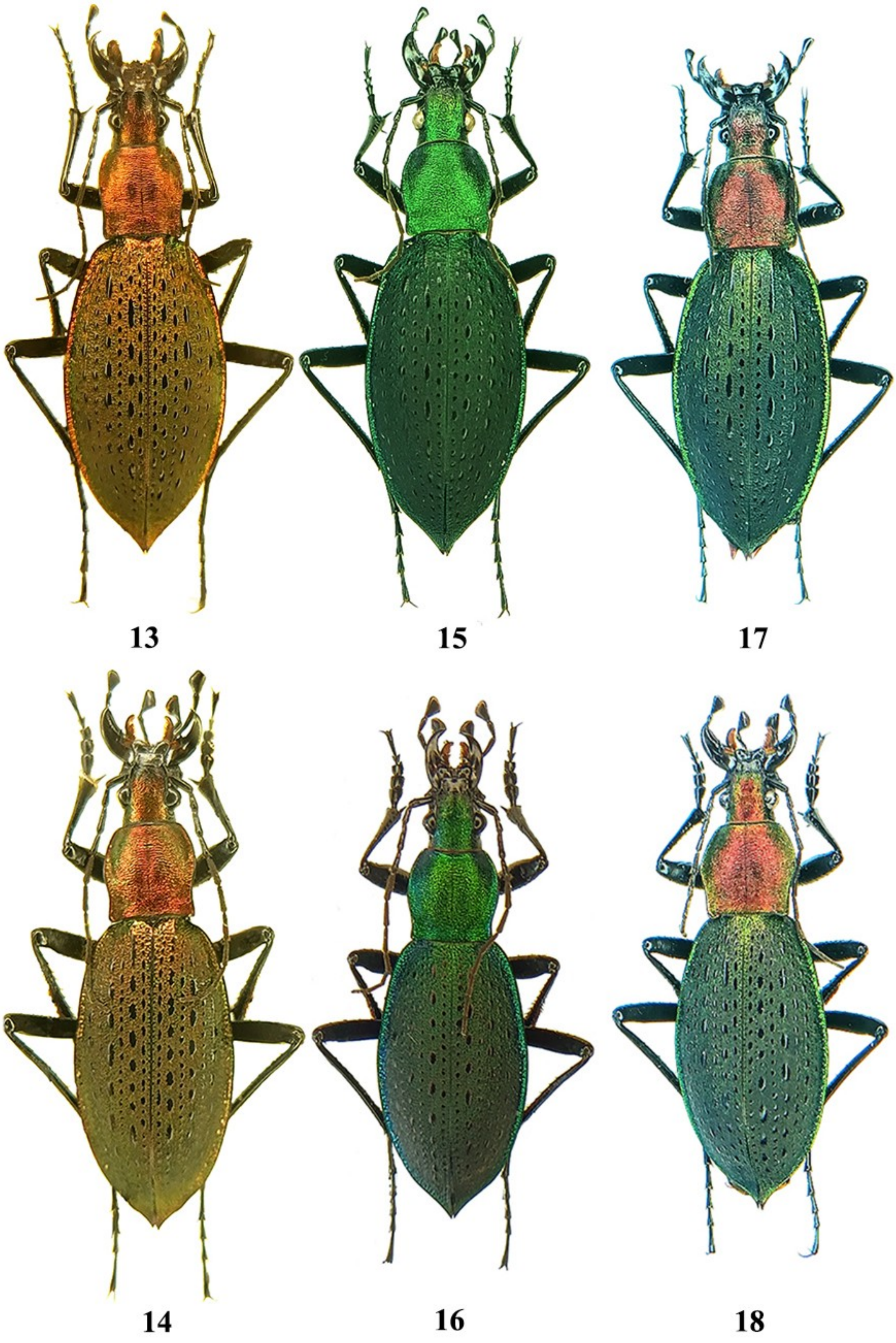

Fig.13-18 : F1 hybrids. – 13, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus branickii*). – 14, ♂ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus branickii*).– 15, ♀ (♀*C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus furumiellus*).– 16, ♂ (♀*C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus furumiellus*) .– 17, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus honanensis*). – 18, ♂ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus honanensis*).

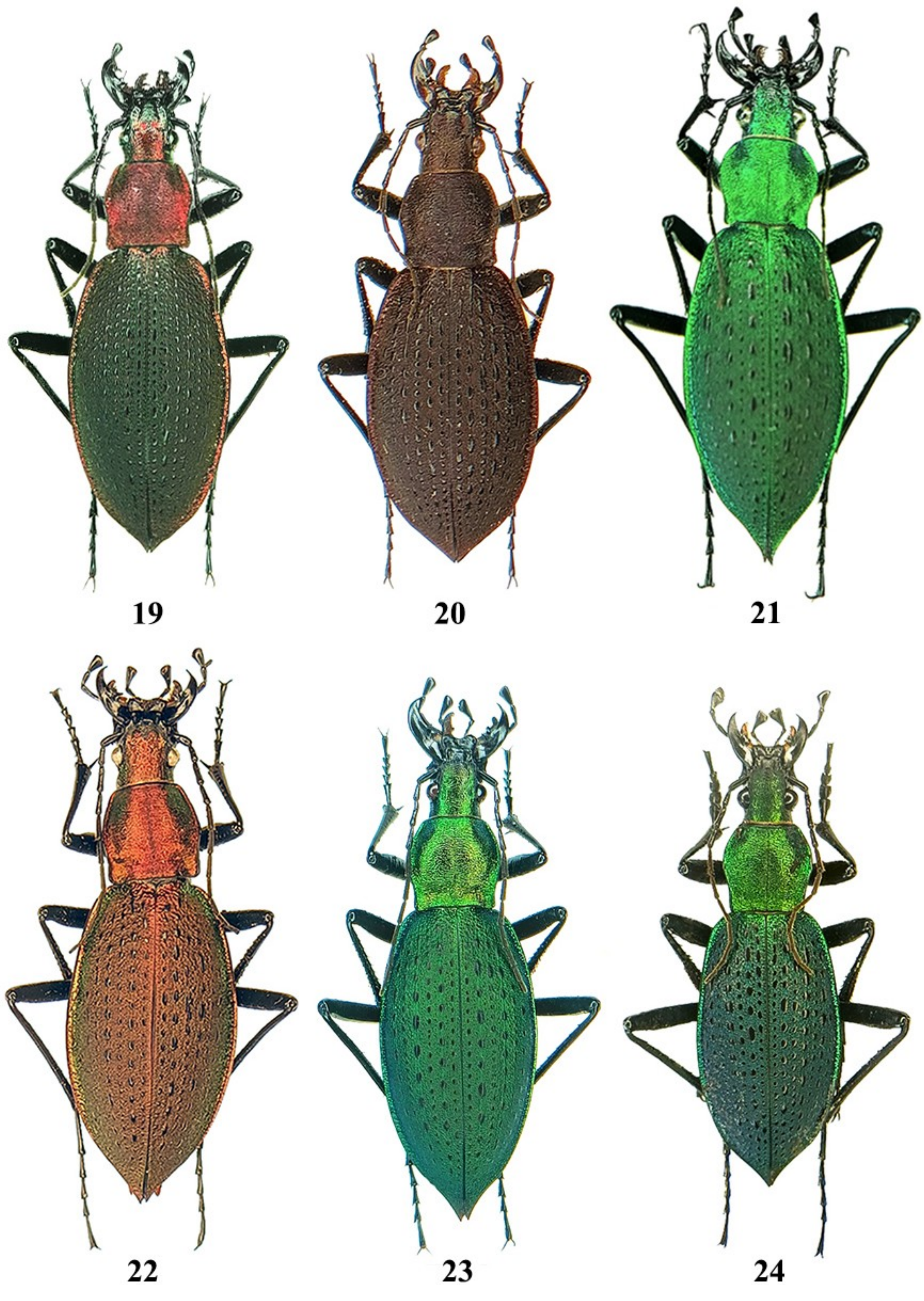

Fig. 19-24 : F2 hybrids. – 19, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus monilifer*). – 20, ♀ (♀ *C. (C.) smaragdinus monilifer* X ♂ *C. (D.) fruhstorferi*). – 21, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus euviridis*). – 22, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus branickii*). – 23, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus furumiellus*). – 24, ♂ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus furumiellus*).

derived from *C. (C.) smaragdinus honanensis,* previous experiments performed several years ago and recent new experiments (shown in Table 2) never afforded any larva. Moreover, the obtained eggs never showed any sign of fertilization.

Crossings leading to F3 hybrids

In order to check if the F2 hybrids keep the fertility observed for F1 hybrids, we engaged some of them in new crossing experiments. We chose the two sets Fsh Smm and Smm Fsh to check if there is no asymmetric male sterility with these hybrids. We added an example with F2 hybrids derived from *C. (C.) smaragdinus branickii* to check the generality of the fertility of these F2 hybrids. As shown in Table 3, the fecundity of the F2 females is in the same range as for F1 hybrid females. Similarly, the prolificity data show that the overall fertility of these F2 hybrids remains stable although we can notice a slight decrease in the case of the Smm Fsh crossing.

F3	♀	♂	eggs	L1	imagines	fecundity	prolificity	imagines/eggs
FshSmm	10 F	10 M	94	55	31 (21F 10M)	9.4	0.56	0.32
SmmFsh	4F	3M	84	33	7 (5F 2M)	21	0.21	0.08
FshSmb	9F	10 M	82	36	14 (8F 6M)	9.1	0.38	0.17

Table 3: Data obtained for F3 hybrids.

Discussion

The breeding of *C. (D.) fruhstorferi* Roeschke, 1900, and *C. (C.) smaragdinus* Fischer, 1823, shows that these species behave like most species of the subgenus *Damaster* and *Coptolabrus*. In particular, the diet (mainly composed of *Thebapisana* Müller, 1774), the number of larval stages (2) as well as the durations of the various pre-imaginal stages are quite comparable to those observed for the other *Coptolabrus* and *Damaster* species that we have bred. The ability to get well-shaped and healthy F1 hybrids between these two species is observed for the five *C. (C.) smaragdinus* subspecies studied. As expected, the phenotypes of these F1 hybrids are closely related and show intermediate features transmitted by the parent species. In particular, the dominant color of the elytra is reminiscent of that of the parent *C. (C.) smaragadinus* ssp. This color is more pronounced on live specimens. The elytral sculpture shows relatively unmarked primary intervals compared to *C. (C.) smaragdinus*. *C. (C.) smaragdinus monilifer* is the less elongated subspecies among the different *C. (C.) smaragdinus* parents. It is interesting to notice that this feature is

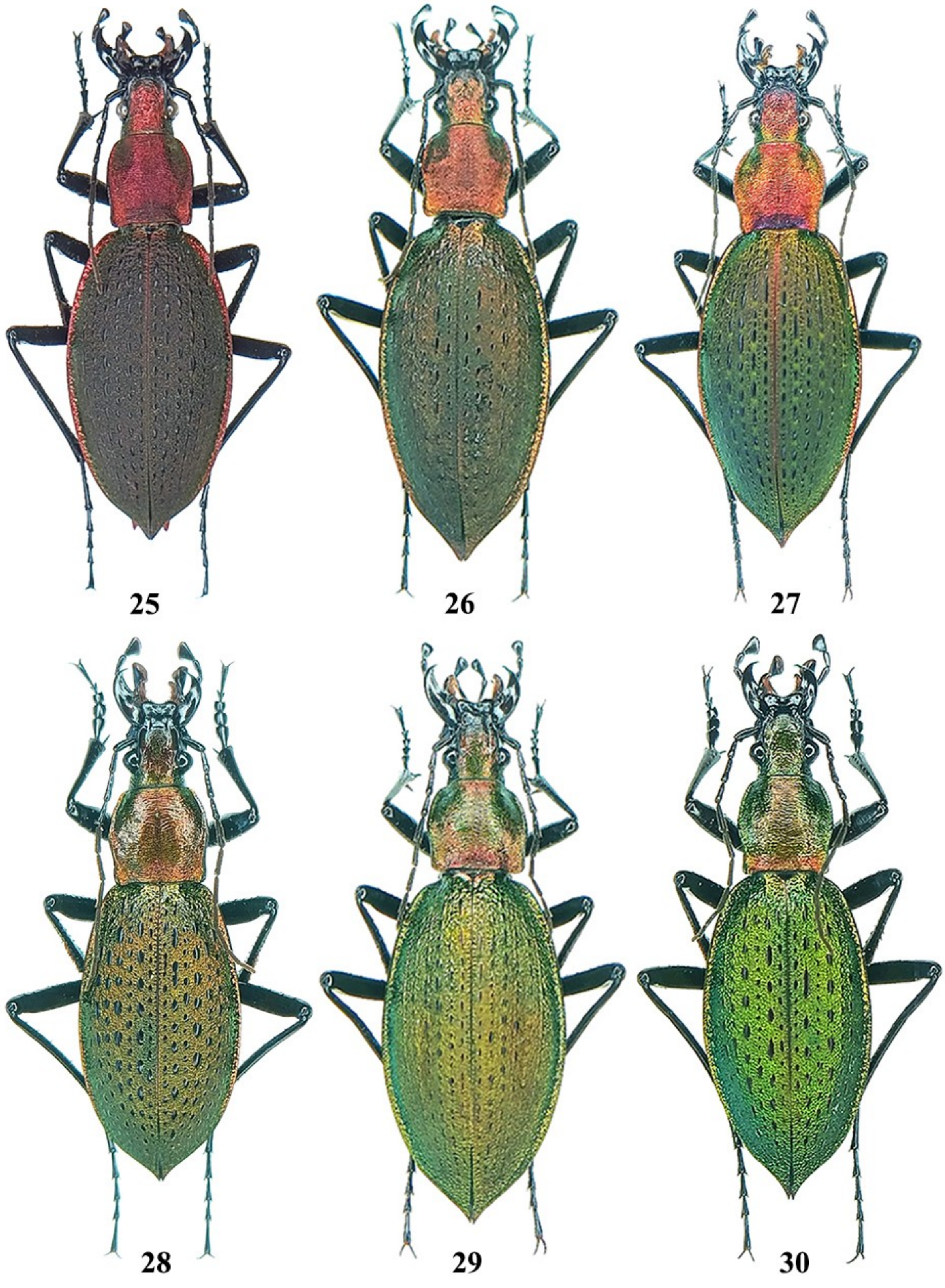

Fig. 25-30 : Color variation of F2 hybrids, ♀ and ♂ (♀ *C. (D.) fruhstorferi* x ♂ *C. (C.) smaragdinus branickii*).

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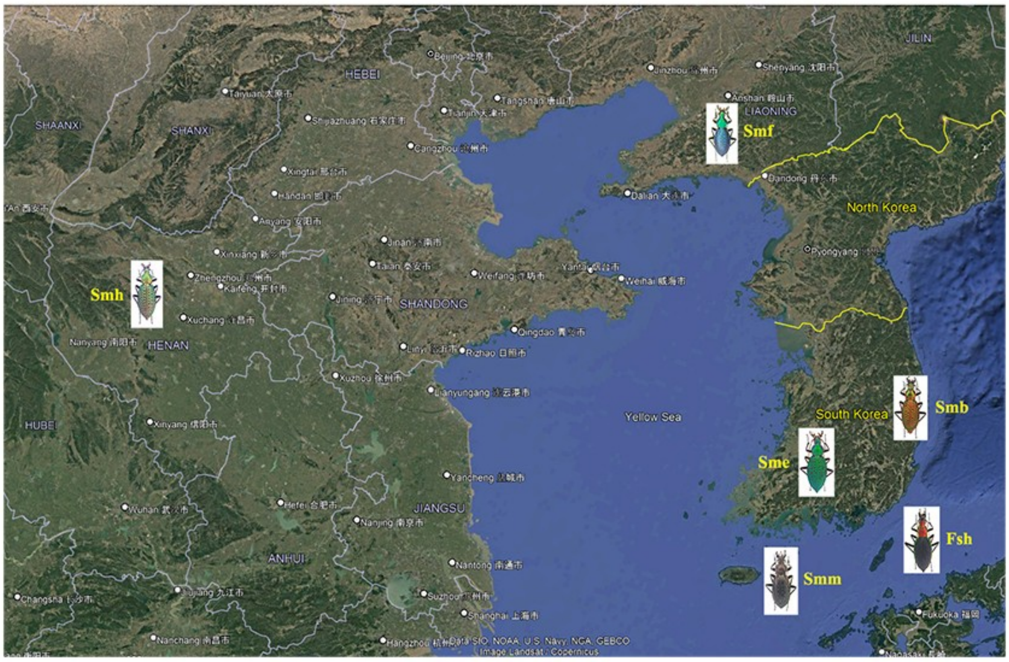

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Fig. 31-34 : F3 hybrids. – 31, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus monilifer*). – 32, ♀ (♀ *C. (C.) smaragdinus monilifer* X ♂ *C. (D.) fruhstorferi*). – 33, ♀ (♀ *C. (D.) fruhstorferi* X ♂ *C. (C.) smaragdinus branickii*). – 34, Localities of taxa used for crossing experiments *(Background image extracted from Google Earth Pro, cropped and annotated by the authors. © 2025 Google / Maxar Technologies).*

transmitted to F1 generation leading to hybrids with a rather chunkier shape and showing no or a very tiny mucron. This specific shape seems to be transmitted when F1 hybrid is derived from a female *C. (C.) smaragdinus monilifer* but is absent on hybrids obtained in the opposite direction (see Fig. 7-10). This phenomenon seems to be genetically transmissible as shown by F2 and F3 hybrids shown in Fig. 19, 20, 31 and 32. Such a behavior has already been described during the experimental crossings of *C. Cathoplius* species (Busato *et al.*, 2014).

It is worth noting that we could obtain hybrids whatever the direction of crossing with all studied *C. (C.) smaragdinus* subspecies. These results are consistent with a rather close genetic proximity of all these taxa.

However, the fertility observed when crossing F1 hybrids derived from the Korean *C. (C.) smaragdinus euviridis* was more surprising. Indeed, most of our attempts to get F2 generation derived from F1 *Coptolabrus* or *Damaster* hybrids generally failed (in the *Carabus* genus, male is heterogametic so the corresponding hybrid is usually sterile – Haldane's rule). For example, we recently tried to cross F1 hybrids *C. (D.) fruhstorferi* x *C. (D.) jankowskii taebeagsanensis* without success.

So, it was interesting to investigate more subspecies to know if this interfertility of F1 is a general trend for different *C. (C.) smaragdinus* ssp. populations located at distances more or less distant from that of *C. (D.) fruhstorferi,* endemic to Tsushima Island (see Fig. 34). Asymmetry of fertility has been observed for diverse cases of hybridizations (Gomes *et al.,* 2014; Su *et al*., 2006; Mardiros *et al.,* 2016). Moreover, we studied crossings between different *C. (C.) smaragdinus* subspecies and noticed some cases of asymmetric fertility. For example, *C. (C.) smaragdinus euviridis* crossed with *C. (C.) smaragdinus honanensis* give nice F1 but these ones are interfertile affording F2 individuals only by crossing *C. (C.) smaragdinus honanensis* female by *C. (C.) smaragdinus euviridis* male but the crossed individuals F1 obtained in the opposite direction did not give any F2 larva, likely due to the sterility of males involved in this crossing. It is the reason why we made all crossings in both directions except for *C. (C.) smaragdinus furumiellus* due to lack of virgin female. As shown in Table 2, the fertility of F2 hybrids is a general property except for two subspecies. In the case of hybridizations involving F1 *C. (D.) fruhstorferi* x *C. (C.) smaragdinus furumiellus*, the female fecundity is among the best compared to other F1 hybrid females. However the number of larvae and the prolificity are very low and the number of F2 imagines is only two. Finally, the two crossings using *C. (C.) smaragdinus honanensis* did not afford any larva and no sign of fertilization was observed in eggs. That strongly suggests a sterility of the corresponding F1 Fsh Smh and Smh Fsh males.

Although, we must be careful about these data due to the relatively small number of individuals used for these crossings, it seems that there is a probable correlation between the overall fertility of the F1 hybrids and the distance between Tsushima Island and the localities of the different *C. (C.) smaragdinus* ssp. All the Korean *C. (C.) smaragdinus* ssp. give fertile F1 hybrids (in both directions). It is remarkable that *C. (C.) smaragdinus monilifer* which is endemic to Jeju Island leads to very prolific F1 hybrids. That is probably related to the proximity of this volcanic island and Tsushima Island which were connected to the Korean peninsula during the last glaciation periods (Lee, 2008). However, the Chinese *C. (C.) smaragdinus furumiellus* coming from Liaoning gave F1 hybrids which proved to be poorly fertile. The distance between Tsushima Island and the Liaoning province (c.a. 1000 km) can explain this decrease of genetic proximity. The same explanation may account for the sterility of F1 hybrids derived from the most distant *C. (C.) smaragdinus honanensis* population (c.a. 2000 km).

Finally, the possibility to get a third generation of hybrids as shown in Table 3 and Fig. 31-33 reinforces the hypothesis of the high genetic proximity of the corresponding species.

These *in vivo* data are in good agreement with the information published by Osawa (S.), Su (Z.-H.), Imura (Y.) (Chapter 5, p. 88). Based on mitochondrial ND5 gene, these authors constructed a phylogenetic tree where *C. (D.) fruhstorferi* and *C. (C.) smaragdinus* are located on the same branch of the *Coptolabrus* tree. Though constructed on a mitochondrial gene, these data seem to be coherent with our results. However, it would be very interesting to use more relevant nuclear genes such as *Wg* and *PepCK* (Sota *et al*., 2004) to see if the same phylogenetic proximity is found.

Our results led us to suppose that these two species had a common ancestor in a relatively recent past. The modulation of the fertility observed with the distance of the genitors could indicate that the process of speciation is not yet fully completed, in particular in the Korean peninsula populations.

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