

Identity of the groundnut and tamarind seed-beetles (Coleoptera: Bruchidae: Pachymerinae), with the restoration of *Caryedon gonagra* (F.)

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Abstract – The study of seed-beetles feeding on groundnuts (*Arachis hypogaea*), tamarind (*Tamarindus indica*) and other Caesalpinioideae from various areas of the Old World, enables the authors to characterize two different species of *Caryedon* that are usually confused. *C. serratus* (Ol.), usually known as the « groundnut seed-beetle », feeds on seeds of tamarind and various wild Caesalpinioideae in the genera *Piliostigma*, *Cassia* and *Bauhinia*. It is present in West and Central Africa. Detailed morphological studies associated with the analysis of part of the Cytochrome B gene show that another species, *Caryedon gonagra*, infests tamarind and other Caesalpinioideae in Egypt, South Asia, Australia and New Caledonia; this species also feeds in the seeds of a few Mimosoideae in the genera *Acacia*, *Albizia* and *Dichrostachys*. *Caryedon gonagra* and *C. serratus* appear as sister species deriving from an ancestor that may have fed on both Mimosoideae and Caesalpinioideae. Contrary to what happens in *C. serratus*, it seems that *C. gonagra* does not infest groundnuts under natural conditions. Larval development in groundnuts under laboratory conditions is however possible, as in several other *Caryedon* species.

Résumé – Identité des bruches de l'arachide et du tamarin (Coleoptera: Bruchidae: Pachymerinae) et réhabilitation de *Caryedon gonagra* (F.) – L'examen de bruches ayant pour plantes-hôtes l'arachide (*Arachis hypogaea*), le tamarin (*Tamarindus indica*) et d'autres Césalpinioïdées, en provenance de diverses parties de l'ancien monde, permet aux auteurs de mettre en évidence deux espèces distinctes de *Caryedon* habituellement confondues. *C. serratus* (Ol.), communément appelée « bruche de l'arachide », a pour hôtes les graines de tamarinier et de diverses Caesalpinioïdées sauvages appartenant aux genres *Piliostigma*, *Cassia* et *Bauhinia*; elle est répandue en Afrique de l'Ouest et en Afrique Centrale. Une étude morphologique approfondie, associée à l'analyse d'une partie du gène du Cytochrome B, révèle qu'en Egypte, dans toute l'Asie du Sud, en Australie et en Nouvelle Calédonie, c'est une autre espèce, *Caryedon gonagra* (F.), qui infeste le tamarin et diverses autres Césalpinioïdées; cette espèce possède également pour hôtes quelques Mimosoïdées dans les genres *Acacia*, *Albizia* et *Dichrostachys*. *Caryedon gonagra* et *C. serratus* apparaissent ainsi comme des espèces sœurs dérivant d'un ancêtre dont on peut supposer qu'il se nourrissait à la fois de Mimosoïdées et de Césalpinioïdées. Contrairement à ce qu'on observe pour *C. serratus*, il ne semble pas que *C. gonagra* infeste l'arachide en conditions naturelles. Cependant, comme chez plusieurs autres *Caryedon*, le développement larvaire est possible au laboratoire.

The identity of the groundnut seed-beetle *Caryedon serratus* (Olivier, 1790) was established by Decelle, who published a comprehensive synonymy in 1966. It has a small number of native host plants in Africa: *Bauhinia rufescens*, *Piliostigma reticulata*, *P. thonningii*, tamarind (*Tamarindus indica*), which all belong to the Leguminous subfamily Caesalpinioideae. Less than one century ago, it has added the introduced groundnut (*Arachis hypogaea*) (Leguminosae Papilionoideae) to its diet, thus becoming one of the major African insect

pests. The problem is still spreading in some parts of the continent (see Delobel 1995 for a discussion of the probable scenario which led to the present situation). African countries like Niger, Mali, Senegal and Congo derive a substantial part of their national income from groundnut cultivation. In these areas, the presence of the seed-beetle has compelled farmers, traders and national storage facilities to make use of large amounts of insecticides, thus dramatically reducing their annual income. *C. serratus* was recently identified in Australian Queensland as a pest of *Cassia brewsteri*, a source of edible gum (Cunningham & Walsh 2002).

In 1894, Decaux gave a quite precise description of the morphology and biology of a tamarind seed-beetle,

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which he named *Caryoborus tamarindi*. The name *tamarindi* has been in use in Egypt (Shaumar 1963) and in India (Vazirani 19075). In Asia however, the tamarind seed-beetle is usually known as *C. serratus* (Arora 1977), and is sometimes considered as a pest of groundnuts (Vazirani 1975, Dick 1987). *C. serratus* is often also reported as feeding in the seeds of various species of *Acacia* (Mimosoideae) and *Cassia* (Caesalpinioideae) (Mukerji & Chatterjee 1951, Arora 1977, Vir & Jindal 1996). However, Indian specimens of tamarind and/or groundnut seed beetles have often been known as *Caryedon gonagra* Fabricius, 1798. In 1966, Decelle synonymized *gonagra* and *serratus*, partly on the basis of Southgate & Pope's (1957) redescription and illustration of *C. gonagra*.

As early as 1920, Bridwell identified a seed beetle infesting *Prosopis juliflora* seeds in Hawaii as *Caryoborus gonagra* (F.). Several specimens of a species of *Caryedon* also identified as *C. gonagra* (F.) were reared from *T. indica* seeds collected in Tehuantepec, Oaxaca, Mexico, in 1963, and specimens of the same species were intercepted in Texas and California (Johnson 1966). Subsequent reports of the bruchid in the new World were under the name *C. serratus* (Nilsson & Johnson 1992; Romero & Johnson 2002).

We have been able to study specimens of *Caryedon* reared from groundnuts, *T. indica* and other Mimosoideae and Caesalpinioideae in Congo, Ivory Coast, Senegal, Niger, Chad, Egypt, India, Sri Lanka, Thailand, Vietnam, and Australia. We found among these specimens morphological differences that led us to consider that there could be more than one species under the name *serratus*. In order to solve the problem, the DNA of specimens from Africa and Asia was also analyzed.

Material and methods

Most specimens used in this study were obtained from identified seeds samples. Pods of various non-cultivated Leguminosae (Caesalpinioideae and Mimosoideae) and of groundnuts (Faboideae) were collected between 1995 and 2002 following methods outlined by Sembène & Delobel (1998), and additional material obtained from *B. thonningii* pods in Ivory Coast (see Gillon *et al.* 1992) was also studied.

Part of the adult specimens was dry-mounted for morphological studies, and part was preserved in pure ethanol for total DNA extraction. Morphological study comprised extraction of the genitalia, which were cleared and mounted in Canada balsam following standard procedures. As often as feasible, slide preparations of male genitalia were made with internal sac exerted. This gave a clearer view of the different sclerites and spines that are attached to the sac wall and of their relative position. It thus avoided possible misinterpretations due to variable positions of sclerites in variously retracted internal sacs. Slides were studied

Table 1 – Species of Leguminosae sampled, country where collected, and coding used in phylogenetic analysis.

	Senegal (Keur-Baka)	Senegal (Fimela)	Egypt	India	Vietnam	Australia
Caesalpinioideae						
<i>B. rufescens</i>	Br-K	Br-F				
<i>B. variegata</i>			Bv-E			
<i>C. tomentosella</i>						Ct-A
<i>G. triacanthos</i>				Gt-E		
<i>P. reticulatum</i>	Pr-K	Pr-F				
<i>S. didymobotrya</i>			Sd-E			
<i>T. indica</i>	Ti-K	Ti-F	Ti-E	Ti-I	Ti-V	
Mimosoideae						
<i>A. t. raddiana</i>			Ar-E			
<i>D. cinerea</i>			Dc-E			
Faboideae						
<i>A. hypogaea</i>	Ah-K	Ah-F				

through a Leica DM LS light microscope and photographs were taken with a Nikon Coolpix 990 digital camera. Drawings were made with Adobe Illustrator 9.0, using photographs as models.

Specimens used for DNA analysis were reared from various leguminous pods collected in the following localities (Table 1): in Senegal *Bauhinia rufescens*, *Piliostigma reticulatum*, *Tamarindus indica* and *Arachis hypogaea* pods in two locations: Keur Baka and Fimela. Egyptian specimens were reared from *Gleditsia triacanthos* in Cairo (Gt-E1 to 4), *Senna didymobotrya* in Bahareya (Sd-E1 and 2), *Bauhinia variegata* in Cairo (Bv-E1 to 6), *Tamarindus indica* in Bahareya, *Acacia tortilis raddiana* from Bahareya and *Dichrostachys cinerea* from Cairo. Indian specimens were reared from *T. indica* in Pondicherry, Vietnamese specimens from *T. indica* in Ho-Chi-Minh City, Australian specimens from *Cassia tomentella* in Biloela, Queensland. The outgroup was *Decellebruchus (Bruchidius) atrolineatus* (Pic), an African species belonging to subfamily Bruchinae. *Caryedon lunatum* Prevet, a West African species which feeds in *Combretum* (Combretaceae) seeds was also included in the study.

Total genomic DNA was extracted from prothorax of individual seed-beetles as described elsewhere (Vogler & DeSalle 1993). A partial Cyt. B end region was PCR-amplified with primers CB1 (5'-TATGTACTACCATGAGGACAAATATC6-3') and CB2 (5'-ATTACACCTCCTAATTTATTAGGAAT-3'). The 25 µl PCR reaction mixture contained 2.5 µl enzyme buffer, 2.5 mM MgCl₂, 0.6 unit of Taq polymerase, 17.5 pM of each primer, 25 nM of dNTP and 1 µl of DNA extract. After an initial denaturation step at 92°C for 3 min, reactions were submitted to 35 cycles of 1 min at 92°C, 1 min 30 s at 48°C and 1 min at 72°C. A pool of two PCR was concentrated and loaded on a 1.3 agarose gel. The PCR gel band was cut and then purified with Quiaquick PCR gel purification kit (Qiagen), and directly sequenced on an Abi 373 automated sequencer using TaqFS and Dye-labeled terminators (Perkin-Elmer). Sequence alignment was performed using ClustalW (Thompson *et al.* 1994). Aligned sequences were entered in McClade 3.06 (Maddison & Maddison 1992) for subsequent treatments.

Resulting data were subsequently used to calculate Kimura 2-parameter genetic distances and to analyze phylogenetic rela-

tionships by maximum-parsimony (MP) and neighbor-joining (NJ) methods. Phylogenetic analyses were conducted using PAUP 4.0 (Swofford 1998). The MP analysis was done with the heuristic search option on 50 random stepwise taxon addition replicates, using the branch swapping tree bisection-reconnection (TBR) option. The consistency index CI and the retention index RI (Farris, 1994) were also calculated. A bootstrap procedure (1000 iterations with the same option of heuristic search) was used to establish the score of each node (Felsenstein 1985) by retaining groups compatible with the 50% majority rule consensus. The neighbor-joining tree was performed from the DNA distance matrix calculated under the selected model, and the robustness of inferences was assessed through bootstrap resampling (1000 replicates). Analyses were also performed on the amino acid sequences, both with MP and NJ methods. The Shimodaira-Hasegawa test (Shimodaira & Hasegawa 1999) using real bootstrap with 1000 replications was used to test for a significant difference between the scores of the different trees obtained.

All relevant insect material, except as mentioned, is preserved in the IRD collections at the Museum national d'Histoire naturelle (MNHN), Paris, and in the insect collection of the Centre de Biologie et de Gestion des Populations (CBGP), Montpellier.

RESULTS

1. Phylogenetic relationships

Sequences of the partial Cyt. B gene (442 bp) in 22 *Caryedon* populations are available on request. All 442 bp sequenced were used in the analysis described below. The alignment was straightforward and involved no insertions/deletions. The sequences could be unambiguously aligned. Of these sites, 93 were variable and 86 were parsimony informative. The number of nucleotide differences in pair-wise comparisons in Egyptian populations ranged from 0 to 1.9%. In Senegalese populations, this number ranged from 0 to 7.0%. Between Senegalese and Egyptian populations, the number of nucleotide differences in pair-wise comparisons ranged from 14.3 to 19.7%.

Within the oriental group, genetic distances ranged from 0% (between Egyptian populations reared from *T. indica* and those reared from *Bauhinia variegata*) to 8.2% (between populations reared from *T. indica* in India and in Vietnam). Within the Senegalese group, genetic distances ranged from 0% (between populations reared from *Arachis hypogaea* and populations reared from *Piliostigma reticulatum*) to 10.1% (between populations reared from *Arachis hypogaea* and those reared from *B. rufescens*).

The MP analysis on nucleotide data yielded 54 equally parsimonious trees that were 373 steps long (CI = 0.774; RI = 0.695). The strict consensus of these trees

is presented in figure 1. The NJ analysis is presented in figure 2. The topologies obtained with MP and NJ methods were compared using the Shimodaira-Hasegawa test and the Wilcoxon's signed-Rank test. These tests did not provide support for a significant difference between the trees. The MP analysis on amino acid data yielded 65 trees of 299 steps. These trees (not shown) displayed groups already identified by previous analyses. Bootstrap values were all statistically significant (over 70%), and showed two very well defined clades, one for Senegalese specimens, whatever their host, the second for Egyptian and Asian specimens. Structuration according to host was clear in both trees: the MP tree (fig. 1) confirmed results given by Sembène & Delobel (1998) for Senegalese specimens, and in particular the relative genetic isolation of populations on *B. rufescens*, and the close relationship existing between *P. thonningii* and *A. hypogaea* populations.

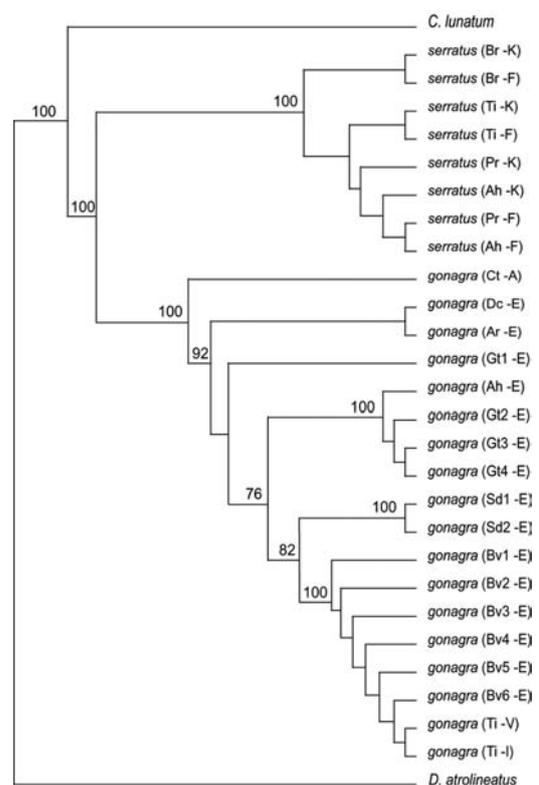


Figure 1

Phylogenetic relationships among nucleotide sequences of the partial Cyt. B gene of 26 specimens of the *Caryedon* spp. group using maximum parsimony. *Decellebruchus (Bruchidius) atrolineatus* is the outgroup (see table 1 for abbreviations). Tree was generated by a heuristic search (PAUP 4.0b4a) on saturated substitution. Numbers above branches are % bootstrap values (1000 replicates). This tree is the strict consensus of 54 most parsimonious trees.

Oriental samples showed a rather similar trend, with well defined *G. triacanthos* populations, and a large clade bringing together all specimens reared from *B. variegata* and *T. indica* (except Vietnamese specimens). Insects reared from Mimosoideae (Ar-E and Dc-E) clumped together, and the position of Vietnamese and Australian specimens showed a higher level of isolation.

The genetic distance between *C. serratus* and *C. gonagra* was computed from a portion of the Cyt. B gene that was successfully used to distinguish species in the rodent genus *Praomys* (Lecompte *et al.* 2002), or aphids in the genus *Aphis* (Cœur-d'Acier, unpublished). Our data indicate that Senegalese and Oriental specimens of *Caryedon* belong to two distinct clades. Egyptian specimens reared from *A. tortilis raddiana*, *D. cinerea* and *G. triacanthos* seem to belong to strongly differen-

tiated populations, but their degree of homology with *T. indica* and *B. variegata* populations would not justify their treatment as distinct species. Similarly, geographical isolation seems to have occurred in Vietnamese populations feeding in *T. indica* seeds and Australian populations feeding in *C. tomentella* seeds.

2. Morphological analysis

A careful study of the external and genital morphology showed that variation occurred between samples of different geographic origins. Color appeared as rather variable within populations, the density of dark markings ranging from almost absent, with entirely reddish-brown elytral integument, to very dense black mottling on elytra, almost entirely black underside, and legs variously dotted with black. A constant trend however existed in the colour of legs, with Egyptian and Asian specimens showing more contrasted femora and tibiae. Interesting diagnostic characters were the shape of the hind femur, which was more or less oblong, and the number of teeth of its ventral pecten. Morphology of male genitalia provided several diagnostic characters, in particular the detailed morphology of sclerites in the internal sac and the size and density of spines in its apical part: they were large and numerous in African specimens, smaller and much less numerous in Asian specimens. Female genitalia, particularly the relative size of dorsal and ventral vaginal sclerites, also showed constant differences: in West African specimens, these sclerites were almost equal in size, whereas Oriental specimens had a much smaller dorsal sclerite. Size and density of spines in the *bursa copulatrix* were also a good diagnostic character.

3. Species redescription

Both genetic and morphological data indicated that specimens of West and Central African origin and specimens originating from Egypt, Southern Asia, Australia and New Caledonia belong to two clearly distinct species, the redescription of which follows.

Caryedon serratus (Olivier, 1790)

(figs. 3, 5)

Bruchus serratus Olivier, 1790: 199.

Caryoborus serratus (Ol.): Gyllenhal 1833.

Pachymerus acaciae Gyllenhal, 1833: Roubaud 1916; Hoffman 1945, etc. (misidentification)

Caryoborus fuscus Bedel, 1901, *partim*, (*nec* Goeze, 1777): Decelle 1966

Pachymerus sicutensis Pic, 1924: Decelle 1966.

Caryedon cassiae (Gyllenhal): Decelle 1951 (misidentification).

Caryedon fuscus (Goeze): Mukerji, Menon & Chatterjee, 1957 (misidentification).

Caryedon fuscus Mukerji, Menon & Chatterjee, 1957 (*nec* Goeze): Southgate & Pope 1957 (as a synonym of *C. gonagra*).

Caryedon gonagra (F.): Prevet 1965 (misidentification).

Caryedon serratus (Olivier): Decelle 1966, *partim*.

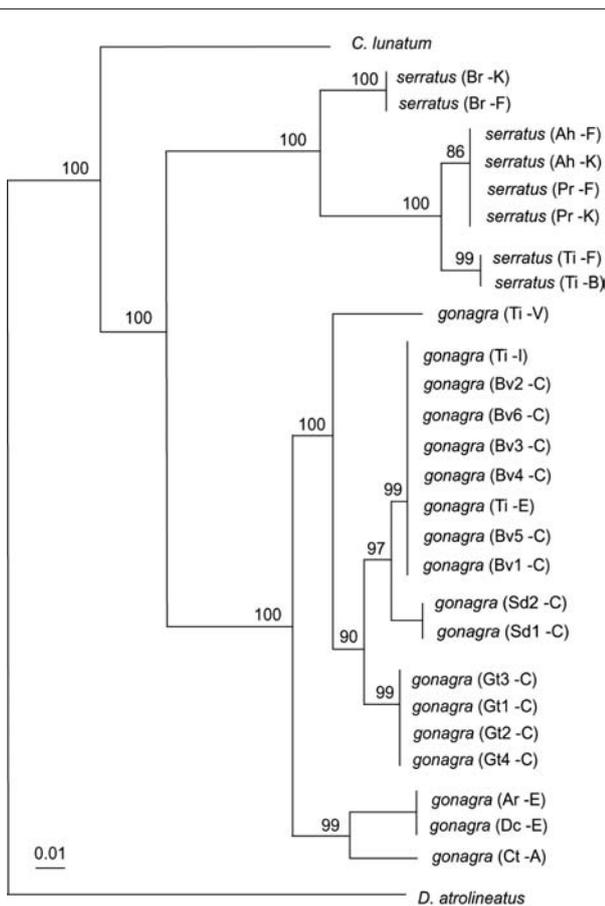


Figure 2

Phylogenetic relationships among nucleotide sequences of the partial Cyt. B gene of 26 specimens of the *Caryedon* spp. group using the Neighbour-Joining method. *Decellebruchus* (*Bruchidius*) *atrolineatus* is the outgroup (see table 1 for abbreviations). Tree was generated on DNA distance matrix. Numbers above branches are bootstrap values (1000 replicates). This tree is the strict consensus of 52 most parsimonious trees.

Type material. Lectotype designated by Decelle (1966), not examined. Type locality: Senegalia (Senegal) (Naturhistoriska Riksmuseet Museum, Stockholm, Sweden).

Material examined. The genitalia of the following specimens were examined: CHAD: région de N'Djamena, ex gousses de *Tamarindus indica*, 19 avril 1996, 1♂, 1♀ (*M. Mbaiguinam*). CONGO: ex semin. *Piliostigma thoningii*, Bikouka, 6 juin 1988, 4♂; Youlou-Mbembe, août 1985, 3♂, 1♀; Kilantari, avril 1985, 2♂, 2♀; Tao-Tao, août 1985, 3♂; Brazzaville, arachide, 3♂, 2♀ (*A. Delobel*). IVORY COAST: Lamto – RCI, 5°02'W 6°13'N, ex sp. 33 [*Piliostigma thoningii*], 25-I-1981, various emergence dates, 1♂, 1♀ [CBGP]. MALI: novembre 2002, 1♀ (*M. Sembène*). NIGER: Niamey, novembre 1991, ex *B. rufescens*, 2♂, 1; idem, ex *Piliostigma reticulatum*, 2♂, 1♀; idem, ex gousse *Arachis hypogaea*, 2♂, 2♀ (*A. Delobel*). SENEGAL: Kaffrine, arachide, 2 janvier 1995, 1♂, 1♀; Keur Baka, décembre 1996, ex *Arachis hypogaea*, 2♂, 1♀ (*A. Delobel*); Dakar, 27 septembre 1999, 1♂; Ngazobil, 30 mars 1996, gousse de *Tamarindus indica*, 2♂, 2♀; Fimela, gousse de *Tamarindus indica*, 6 janvier 1996, 1♂, 1♀; Dakar, marché, *Tamarindus indica*, 16 octobre 1994, 3♂, 2♀ (*H. & A. Delobel*); Keur Baka, ex graine *Piliostigma reticulatum*, 1 juillet 1999, 1♂ (*M.T. Gueye*); Nianing, ex gousse *Piliostigma reticulatum*, 14 novembre 1998, 2♀; Birkelane, *P. reticulatum*, 2 janvier 1995, 3♂; Bandia, *P. reticulatum*, 17 décembre 1994, 2♂, 3♀ (*H. & A. Delobel*). TOGO: Lomé, ex gousse de *Piliostigma thoningii*, 28 août 1995, 1♀ (*I.A. Glitho*).

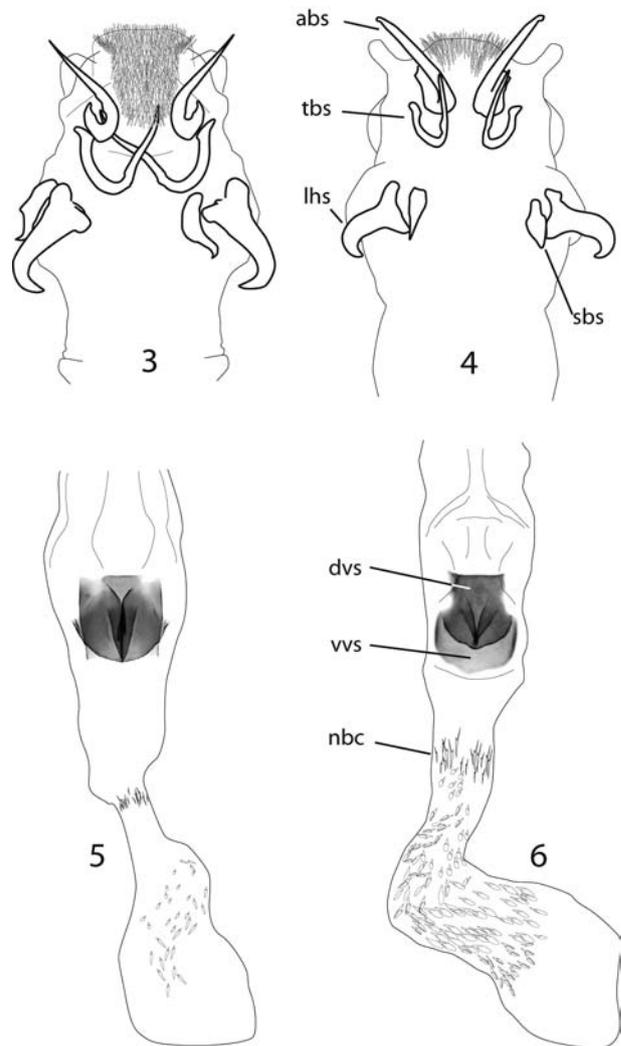
Diagnosis – A large species, greyish-brown with small black spots. Hind femur 2.0 to 2.2 times longer than wide, with pecten of about 10-12 teeth and prepectal teeth visible. Male and female genitalia as shown in figs. 3-5.

Redescription – Length: 3.7-6.2 mm, width: 1.9-3.2 mm (excluding head). Fresh insects have a greyish brown color. The integument is reddish with small, scattered black or dark brown spots, merging here and there into larger, irregular spots. Antennae and legs (except hind femora and tibiae) slightly paler. Antennomeres 1 and 5-11 often darker on disk. Vestiture dense, but not quite covering integument, recumbent except for a few erect setae, specially on pygidium. Setae pale greyish over red parts of the integument, and blackish or dark brown over dark spots. A few areas with denser dark spots: apical third of elytra, especially along suture, basal half of pygidium, ventro-apical part of hind femora; first abdominal sternites often almost entirely black. Fore and median legs sometimes with apex of femur and base of tibia diffusely darker. Pronotum often devoid of black spots. Apex and median line of pygidium with whitish setae. Coloration variable among individuals: a few entirely black specimens have been found in Congo and Ivory Coast; other specimens have a yellowish instead of reddish ground color, and are almost devoid of dark spots.

Male. Head short, constricted behind eyes; eyes bulging, maximum head width about 1.7 times width behind eyes; ocular sinus well defined; eye width about 2.5 times minimum distance between eyes; sharp median longitudinal carina on frons, vertex without interocular tubercle. Antennae reaching basal fifth of elytra; antennal segments 1-4 cylindrical, segments 5-10 serrate,

segment 11 oblong; segment 1 about twice as long as segment 2, segment 3 1.6 times longer than 2, segment 4 hardly shorter than 2, segments 5-10 as long as antennomere 1 (9-10 slightly longer), but widened at apex; segment 11 1.4 times longer than 1, and about 2.8 times as long as wide.

Pronotum about 1.6 to 1.7 times as wide as long, with greatest width at base, sides almost parallel at base, straight or slightly concave, then abruptly converging at about two third of their length, disc feebly convex; punctures on disc irregularly spaced, setous; distances between punctures varying from 1 to 3 diameters; cuticle between coarse puncturation with fine punctures.



Figures 3-6

Male genitalia: ventral view of everted median lobe. The distal part of the internal sac and the ostium are not shown. lhs: large fishhook-like sclerite; sbs, small basal sclerite; tbs, thin bent sclerite; abs, apical bent sclerite. – 3, *Caryedon serratus*. – 4, *Caryedon gonagra*.

Female genitalia: distal part of vagina and bursa copulatrix, ventral view. dvs, dorsal vaginal sclerite; vvs, ventral vaginal sclerite; nbc, neck of bursa copulatrix. – 5, *Caryedon serratus*. – 6, *Caryedon gonagra*.

Elytra about 1.5 times as long as their combined width; sides regularly convex; disc convex; striae on disc thin and deep, punctured; punctures elongated, with setae, distances between punctures less or about equal to their diameter; interstriae convex, with strong micropunctuation and a very small number (varying from 0 to 2 per interstria) of coarser punctures.

Legs without sexual dimorphism; hind femora strongly incrassate, at their widest (at base of first spine) 2,2 times longer than wide; mesoventral margin with a series of small teeth not hidden by hair, followed by a pecten of 10-12 sharp teeth, with first tooth 1.5 to 2 times longer than second; hind tibiae strongly arcuate, with 5 carinae complete; apex of hind tibia with mucro about as long as tibial width at apex (lateral view).

Abdomen without modified setae; sternite 5 emarginate to about one third its length; pygidium 1.2 times as long as wide.

Genitalia (fig. 3): internal sac with four pairs of sclerites and a large apical group of dense spines. First pair of sclerites in form of large hooks (lhs); second pair small, located near base of former (sbs); third pair (tbs) thin and pointed, strongly curved; fourth pair (abs) with base hardly enlarged and regularly thinned into a sharp point. Group of apical spines large, composed of both large and long spines mixed with much smaller ones. Ventral and dorsal valves of median lobe approximately of the same shape, ending in a slightly acute angle.

Female similar to male; fifth sternite not emarginate.

Genitalia (fig. 5): dorsal vaginal sclerite large, wide, almost completely sclerotized in its posterior part; ventral sclerite not extending beyond basal part of dorsal sclerite. Spines at neck of *bursa copulatrix* small, those in proximal part thin and less numerous than in *C. gonagra*.

Host plants – Caesalpinioideae: *Bauhinia rufescens*, *Piliostigma reticulata*, *Piliostigma thonningii*, *Tamarindus indica*. Faboideae: *Arachis hypogaea*. In Nigeria, Preveit (1965, under *C. gonagra*; 1967, under *C. serratus*) reared *C. serratus* from these hosts and also from *Cassia arereh*. Specimens reared from seeds of *Cassia sieberiana* in Senegal belong to a distinct though very similar species (Sembène *et al.*, in preparation). *C. serratus* is sometimes recorded as feeding in seeds of various Mimosoideae in Africa: *Acacia nilotica* in the Sudan (El-Atta 1993); *Acacia gerrardii* in Uganda (Mucunguzi 1995); *Faidherbia albida* in Nigeria (Lale & Igwebuikwe 2002). These records are very dubious because these Mimosoideae are the hosts of different species of the *serratus* group which can easily be misidentified (Nongonierma 1975, Silvain & Delobel 1998). The record of *Acacia nilotica* as a host of *C. serratus* in India (Singal & Toki 1990) may also concern a different species. It is worth mentioning here that *P. thonningii* seeds harbour in Kenya two apparently undescribed species of *Caryedon* (Delobel, unpublished).

Distribution (fig. 7) – Burkina Faso (Varaigne-Labeyrie & Labeyrie 1981), Central African Republic (Koyabay 1988), Chad, Congo (People's Republic, capital

Brazzaville), Congo (Democratic Republic, capital Kinshasa: Decelle 1951), Ivory Coast (Gagnepain & Gillon 1989), Niger, Nigeria (Preveit 1965), Senegal, Togo (Woegan *et al.* 1997), Uganda (Preveit 1967). *C. serratus* is a pest of groundnuts in only part of its area of distribution in Africa (Preveit 1967, Delobel & Matokot 1991). It has also been reported as a pest of groundnuts in India (Vazirani 1975, Dick 1987), but the true identity of these populations remains to be defined. It is often imported with groundnuts in European countries.

We have seen one specimen from Réunion Island: St Paul, Boucan Canot, 5m, 6.v.1952 (J. Hamon), identified as *C. serratus* Ol. by J. Decelle in 1971 [coll. IRD, Paris]; the specimen (a female) lacks genitalia and cannot therefore be assigned to one or the other species with certainty. Specimens from Iran (Anton 1998), Oman (Anton 1994), Israel (Anton *et al.* 1997) are unknown to us, but they probably belong to the following species, *C. gonagra*. Specimens obtained in the New World from various Caesalpinioideae and identified as *C. gonagra* or *C. serratus* (Johnson 1966, Nilsson & Johnson 1992, Romero & Johnson 2002) are unknown to us.

Affinities – *C. serratus* is part of a small group of species with similar genitalia and elytral pattern. Typical of this species are the shape of the larger hooks, the presence of two pairs of thin and strongly curved sclerites at apex of internal sac. It is most closely related with *C. acaciae* sensu Decelle, from which it may be distinguished by the absence of modified setae on the first two abdominal sternites. It is also closely related with *C. longispinosus* Decelle *in litt.* (Nongonierma 1975, Silvain & Delobel 1998, Delobel *et al.* 2000), a species characterized by a particularly long first tooth of pecten at hind femur, but has a similar genital morphology.

Caryedon gonagra (Fabricius, 1798) (figs. 4, 6)

Bruchus gonagra Fabricius, 1798: 159.

Caryoborus languidus Gyllenhal: M. Decaux 1890.

Caryoborus tamarindi C. Decaux, 1894, **syn. nov.**

Caryoborus gonagra (F.): Bridwell 1920.

Pachymerus notativentris Pic, 1924: 24, **syn. nov.**

Caryedon gonagra (F.): Southgate & Pope 1957.

Caryedon serratus (Ol.): Southgate & Pope 1957, Decelle 1966, partim.

Caryedon tamarindi (Decaux): Vazirani 1974.

Material examined – **Type material:** *Bruchus gonagra*, **female holotype**, «gonagra» [Fabricius' handwriting, black ink on brown rectangular label] (ZMUC). The original description mentions «India orientali» as type locality. The specimen was collected by I.K. Daldorff, who lived in Tranquebar near Pondicherry (Tamil Nadu) between 1790 and 1793 (Zimsen 1964). It may therefore be assumed that the type locality is in this area. *Pachymerus*

notativentris: 1 male, «mvhn (?) Indien» «ex coll. Zacher» [Pic's handwriting] «Museum Paris, coll. M. Pic» «notativentris Pic» [Pic's handwriting]; 1 male, «Caryoborus gonager F.» «Museum Paris, Coll. M. Pic» «Pachymerus notativentris» [Pic's handwriting] «Caryedon serratus (Ol.), Oriental form, det. Anton '96» (genitalia on slide «Caryedon 19.01.96 III»). *Caryoborus tamarindi*: according to Decaux, the seeds of *T. indica* from which his specimens emerged originated from «Indes françaises». There were at the end of the XIXth century five French settlements in India: Mahe (Kerala), Chandannagar (Calcutta), Yanam (Andhra Pradesh), Pondicherry and Karaikal (Tamil Nadu). Because Pondicherry was the capital and main settlement of the French Indies, there is a reasonable probability that Decaux' specimens came from that locality. We failed to locate Decaux' collection, and therefore consider the type(s) as lost. Considering biology, geographic origin, and morphology, the specimens obtained from *T. indica* seeds in Pondicherry are in excellent agreement with Decaux' original description.

Other material – The genitalia of the following specimens were dissected: AUSTRALIA: Queensland, ex seeds *Cassia brewsteri*, 4 février 1998, Site 15, 1♂, 1♀; Queensland, ex seeds *Cassia tomentella*, 5 fév. 1999, Biloela, 1♂ (*D. C. Cunningham*). EGYPT: Bahareya, Bawiti, ex gousses *Tamarindus indica*, 22 mars 2002, 2♀; Cairo, Maadi, 20 sept. 2001, ex gousses *Bauhinia variegata*, 1♂, 2♀; same data but 28 oct. 2001, 1♀; Bahareya, Bawiti, 7 fév. 2002, ex gousses *Senna didymobotrya*, 1♂, 1♀; Cairo, Maadi, 8 juin 2002, 4 nov. 2002, ex gousses *Cassia fistula* 1♂, 1♀; Cairo, Giza, 16 oct. 2001, ex gr. *Dichrostachys cinerea*, 3♀; Cairo, Maadi, ex gousses *Gleditsia triacanthos*, 16 sept. 2001, 1♂, 1♀; Guiza, 18 oct. 2001, 2♂, 2♀; Bahareya, 3 déc. 2002, ex gr. *Acacia farnesiana*, 1♂; Ras Mohammed, ex gousses *Acacia tortilis raddiana*, 22 déc. 2000, 1♀; Bahareya, 19 déc. 2002, 2♂, 1♀ (*G. Fédère*). FRANCE: Lyon, tamarind pods imported from Thailand, février 1981 (*B. Delobel*). INDIA: Pondichéry, Ashram Aurobindo, 4 août 2002, ex gousses *Tamarindus indica*, 2♂, 1♀; Pondichéry, juillet 2002, au filet, 1♂, 3♀ (*D. Roguet*). NEW CALEDONIA: Nouméa, janv. fév. 1955, 1♂, 1♀ (*Rageau*). SRI LANKA: Buduruvagala, fin juillet 2002, ex graines *Cassia* sp., 1♂, 1♀ (*D. Rouse*). VIETNAM: Chau Doc, 7 avril 2003, ex gousses *Tamarindus indica*, 1♂, 1♀ (*H. Delobel*).

Diagnosis – A large, greyish-brown species with small black spots, antennae and legs paler, legs with well defined dark markings. Hind femur 1.8 to 2.1 times longer than wide, with pecten of about 12-17 teeth and prepectal teeth minute, usually concealed by setae. Genitalia as shown in figs. 4-6.

Redescription – Length: 3.4-6.3 mm, width: 1.9-3.4 mm (excluding head). Fresh insects have a greyish brown colour. The integument is reddish with small, scattered black or dark brown spots, merging here and there into larger, irregular spots. Antennomeres 1 and 5-11 often darker on disk. Vestiture dense, but not completely covering integument, recumbent except for a few erect setae, specially on pygidium. Setae pale greyish over red parts of the integument, and blackish or dark brown over dark spots. A few areas with denser dark spots: apical third of

elytra, especially along suture, basal half of pygidium. Fore and middle femora usually with dark ventral mark clearly visible near apex, fore and middle tibiae with dark mark near base, ventro-apical part of hind femora with large and well contrasted black mark, the rest often entirely greyish brown; hind tibiae black or blackish except extreme base and apex, lighter and covered with contrasting whitish setae. First abdominal sternites often almost entirely black. Fore and median legs with apical of femur and central two-thirds of tibia darker. Pronotum often devoid of black spots. Apex and median line of pygidium with whitish setae.

Male. *Head* short, constricted behind eyes; eyes bulging, maximum head width about 1.7 times width behind eyes; ocular sinus well defined; eye width about 4 times minimum distance between eyes; sharp median longitudinal carina on frons, vertex without interocular tubercle. Antenna reaching basal fifth of elytra; antennal segments 1-4 cylindrical, segments 5-10 serrate, segment 11 oblong; segment 1 about twice as long as segment 2, segment 3 1.6 times longer than 2, segment 4 equal to 2, segments 5-10 as long as antennomere 1, but widened at apex; segment 11 about 1.2 times longer than 1, and 2.4 times as long as wide.

Pronotum about 1.6 times as wide as long, greatest width at base, sides almost parallel at base, straight or slightly concave, then abruptly converging at about two third of their length, disc feebly convex; punctures on disc irregularly spaced, setous; distances between punctures varying from 0 to 2 diameters; cuticle between coarse puncturation with fine punctures.

Elytra about 1.5 times as long as their combined width; sides regularly convex; disc convex; striae on disc thin and deep, punctured; punctures elongated, with setae, distances between punctures less or about equal to their diameter; interstriae convex, with strong micropunctation.

Legs without apparent sexual dimorphism; hind femora strongly incrassate, at their widest (base of first spine) 1.8 – 2.1 times longer than wide; mesoventral margin with a series of very small teeth usually completely hidden by hair, followed by a pecten of 12-17 sharp teeth, with first tooth 1.5 to 2 times longer than second, to which it is usually coalescent; hind tibiae strongly arcuate, with 5 carinae complete; apex of tibiae with mucro about as long or slightly longer than tibial width.

Abdomen without modified setae; sternite 5 emarginate to about one third its length; pygidium 1.2 times as long as wide.

Genitalia (fig. 4): internal sac as in *serratus*, but 3rd pair of sclerites with enlarged (spatulate) base and a long, almost parallel-sided stem, slightly curved before the blunt apex. Patch of short spines at apex much less developed than in *serratus*. Ventral valve of median lobe of similar shape as dorsal valve, ending in an almost right angle.

Female. Similar to male; fifth sternite not emarginate.

Genitalia (fig. 6) as in *serratus*, but dorsal vaginal sclerite narrower, only partly sclerotized in its posterior part; ventral sclerite extending beyond apical part of dorsal sclerite. Spines at neck of *bursa copulatrix* large, those in proximal part larger and more numerous than in *serratus*.

Host plants – Caesalpinioideae: *Bauhinia variegata*, *Senna didymobotrya*, *Cassia fistula*, *Cassia brewsteri*, *Cassia*

tomentella, *Tamarindus indica*, *Gleditsia triacanthos*. Mimosoideae: *Acacia tortilis raddiana*, *Acacia farnesiana*, *Dichrostachys cinerea*. Faboideae: *Arachis hypogaea* (only under laboratory conditions). Indian records of this species on *Albizia lebbek* (Arora 1977) and on *Adenanthera falcata* (Decaux 1890) are doubtful. The record of *C. gonagra* on algaroba (*Prosopis juliflora*) seeds by Bridwell (1920) also needs confirmation. A specimen in MNHN originating from Germany bears the following label: «Hamburg Jan. 1931, in Indischen Babla-Schoten». Babla is the Bangladeshi vernacular name of the Indian subspecies of *Acacia nilotica*; considering that Egyptian and Senegalese specimens of *Caryedon* bred from *A. nilotica* seeds belong to different species, this record also needs confirmation.

Distribution (fig. 7) – Egypt, India, Sri Lanka, Thailand, Vietnam, New Caledonia, Australia. Sometimes imported with tamarind pods in European countries.

Remarks – Egyptian specimens obtained from *S. didymobotrya* and *D. cinerea* are significantly smaller than those reared from *T. indica* or *B. variegata*. No further morphological differences could however be found between them. Adult size is directly related to seed size, those of *D. cinerea* being markedly smaller than those of *T. indica*. Pending further evidence, we consider that all specimens belong to a single species, even though size differences may hinder or prevent gene flow between individuals from different host plants.

We could not differentiate on a morphological basis specimens bred in Egypt from the Mimosoideae *A. tortilis raddiana* and *D. cinerea* from specimens from Caesalpinioideae, and we therefore consider them as conspecific. However, as shown by Cyt. B analysis

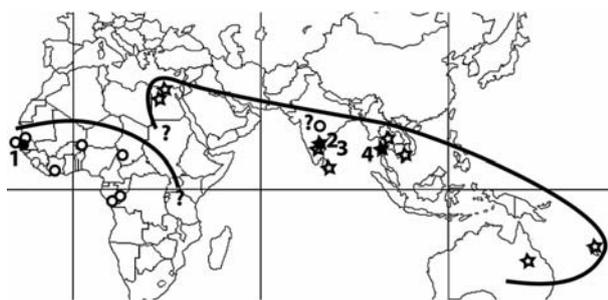


Figure 7
Map showing the geographic origin of studied specimens and the hypothetical distribution of *C. gonagra* (stars) and *C. serratus* (circles). – 1, *C. serratus*. – 2, *C. gonagra*. – 3, *C. tamarindi*. – 4, *C. danielssoni*. Solid symbols indicate type locations.

(figs. 1, 2), they are genetically differentiated from other Egyptian specimens. It may be assumed that some degree of specialization has occurred in populations breeding on these hosts.

Some degree of differentiation seems to exist in populations from Vietnam and Australia, possibly due to geographical isolation. Further studies are needed to correctly evaluate their status. *Caryedon danielssoni* Borowiec, 1990, from Pattaya (Thailand), is a very closely related species. Examination of the genitalia of the type did not show any marked difference with specimens of *C. gonagra*, but *C. danielssoni* has longer and more serrate antennae, which probably justifies its treatment as a distinct species.

DISCUSSION

The confusion between *C. gonagra* and *C. serratus* arose when Southgate & Pope (1957) when studying the type of *C. gonagra* (collected by D. Daldorff, probably in Tranquebar, Tamil Nadu, India, around 1793) wrongly assumed they were dealing with the «groundnut seed-beetle», and disregarded morphological differences documented by Mukerji *et al.* (1957). The latter compared *C. gonagra* (F.) (as *C. gonager*) samples from Pusa (India) with *C. fuscus* (Goeze) (= *C. serratus*) specimens provided by R.W. Howe (Pest Infestation Laboratory, Slough). They described and illustrated male genitalia of both species. Even though the origin of specimens sent by Howe was not mentioned by the authors, it may be assumed they were laboratory-reared groundnut seed-beetles of West African origin. Mukerji *et al.* however concluded that observed differences did not justify the treatment of *C. gonager* and *C. fuscus* as species, but rather as subspecies. The same year, Southgate & Pope (1957) treated the two names as mere synonyms. In 1966, Decelle clarified the status of *C. serratus* but relied on Southgate & Pope's work for the treatment of *C. gonagra*.

Morphological and molecular data (Silvain & Delobel 1998) show that *C. serratus* belongs to a clade of species (including *C. longispinosus* sensu Decelle, *C. mauritanicus* sensu Decelle, *C. excavatus* sensu Decelle, *C. sahelicus* sensu Decelle and *C. acaciae* sensu Decelle) that feed in seeds of Mimosoideae. Feeding on Caesalpinioideae is an apomorphic character in the genus *Caryedon* (Delobel *et al.* 2000). *C. gonagra*, with both Caesalpinioideae and Mimosoideae hosts, has apparently retained (unlike *C. serratus*) some of the characteristics of its mimosoid-feeding ancestors. *C. gonagra* and *C. serratus* thus appear as sister species deriving from an ancestor feeding – like *C. gonagra* – on both Mimosoideae and Caesalpinioideae.

C. gonagra has an ability to infest plants outside the subfamily Caesalpinioideae, and to colonize recently introduced hosts (such as *G. triacanthos* in Cairo). It is worth mentioning here that *C. gonagra* individuals from *G. triacanthos* in Egypt were successfully reared on *A. hypogaea* seeds in the laboratory (Delobel 2002, unpublished data). A number of *Caryedon* species have been reared on groundnuts in the laboratory: *palaestinus* Southgate (Belinsky & Kugler 1978), *crampeli* (Pic), *pallidus* (Olivier), *excavatus* sensu Decelle, *longispinosus* sensu Decelle, *mauritanicus* sensu Decelle (Delobel *et al.* 2000), *gonagra* (Cunningham & Walsh 2002). This has sometimes led authors to consider these species as potential threats to groundnuts (Belinsky & Kugler 1978, Cunningham & Walsh 2002, Vir & Jindal 1996). The rather unique combination of behavioral and physiological traits which enabled *C. serratus* to become a pest of stored groundnuts does not seem however to be present in many *Caryedon* species (Delobel *et al.* 2000). That *C. gonagra* may eventually add (or has already added) *A. hypogaea* to its diet remains however a significant possibility.

In India, there was no sign of groundnut infestation before Dick (1987) reported a heavy infestation of a

groundnut storage facility by a seed-beetle in Kurnool (Andhra Pradesh). Mukerji *et al.* (1957), followed by Vazirani (1975), had to import specimens of *C. serratus* from the Pest Infestation Laboratory in London in order to perform a morphological study of the « true groundnut seed-beetle ». Unfortunately, we did not see Dick's specimens, so that their identity remains unknown. We can hypothesize on a possible introduction in India of *C. serratus*-infested groundnuts, possibly for breeding purposes. On the other hand, groundnut infestations in India may be due to locally adapted populations of *C. gonagra*.

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