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Carabus of Subgenus Cathoplius C.G. Thomson, 1875, with description of their life-way, life-cycle and pre-imaginal morphology (Coleoptera: Carabidae)

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Life-cycle and pre-imaginal morphology in *Carabus* of Subgenus *Cathoplius* C.G. Thomson, 1875 (Coleoptera: Carabidae)

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Short title: Life-cycle and pre-imaginal morphology of Subgenus *Cathoplius*.

Abstract

The authors describe the life-cycle and pre-imaginal characters of the taxa currently ascribed to Subgenus *Cathoplius* C.G. Thomson, 1875, with details never provided before. *Cathoplius* are ground beetles adapted to live in arid environments and extreme habitats such as sub-desert areas. All of them are strictly helicophagous, both during the pre-imaginal stages and as adults, and are localized in a narrow fringe along the Atlantic coast of Northwestern Africa. Several data and observations on the eco-ethology of the different taxa, obtained both in field and in laboratory, are reported. The life-cycle of *Cathoplius* belongs to the winter breeding type, with an extremely high fecundity rate concentrated in a very short period of time, that has no similarity to any other *Carabus* species. Eggs, larvae and pupae of the different species and subspecies of *Cathoplius* are described and illustrated. Hybridization trials between some taxa are also reported, showing a reduced survival rate of the progeny, thus confirming their specific or subspecific differentiation as proposed by classical taxonomy.

Introduction

Representatives of the Subgenus *Cathoplius* C.G. Thomson, 1875, within the Genus *Carabus* Linnaeus, 1758 (in the broad sense), form a very homogenous monophyletic group, which includes ground beetles characterized by strongly sclerified integument, black in color, brachypterous, with elytra that are joined along the suture, an achetous, ellipsoidal, silphoid or cychrized pronotum, and a narrow and very elongate head. These features are typical of strictly helicophagous species

adapted to arid, steppe or sub-desert areas. All of them are localized along the Moroccan Atlantic coast (Fig. 134) and colonize open habitats, such as coastal dunes, steppes and sandy zones with scarce xerophilous vegetation, composed mainly by broom shrubs (in Northern Morocco) or *Launaea arborescens*, *Lycium intricatum* and arboreal spurges shrubs (in Southern Morocco), where snails they prey upon are abundant. Secondarily, they can colonize land modified by man, such as arable fields. Moreover, some populations are known to be present in inland areas (e.g. in Skhour des Rehamna, between Settat and Marrakech, J. Kaláb legit). In Southern Morocco, the southernmost taxon [*C. (Cathoplius) stenocephalus aliai* Escalera, 1944] lives in very localized desert zones that are distant from the Atlantic coast.

According to current taxonomy (Breuning 1932-1937; Deuve 1991; 1994; 2004), Subgenus *Cathoplius* includes two species: *C. (Cathoplius) asperatus* (Dejean, 1826), monotypic, with a Northern distribution, being spread from the outlet of Oued Loukos (Larache) to the outlet of Oued Tensift (South of Safi) (with *cychrocephalus* Fairmaire, 1858 considered as a junior synonym in all catalogues), and *C. (Cathoplius) stenocephalus* Lucas, 1866, the Southern substitutive species, to which the following subspecies are ascribed: *C. stenocephalus stenocephalus*, distributed from Essaouira to Cap Rhir (Tamri) (the population of Cap Rhir is assimilable to the typical form, in spite of being characterized by larger specimens with a more regular elytral sculpture), *C. stenocephalus susicus* Antoine, 1941, distributed from Agadir to Tiznit, *C. stenocephalus ifniensis* (Zarco, 1941), localized in the Sidi Ifni area, and *C. stenocephalus aliai* Escalera, 1944, the Southern desert form, spread from Plage Blanche (South of Guelmim) to Lemsid and Bou Kra (South of Laâyoune).

In contrast, *C. stenocephalus escalerae* Csiki, 1927 (*nomen novum pro laevior* Escalera, 1914 *nec* Krynicki, 1830), described from the area of Meskala (Southeast of Essaouira) and mentioned as a synonym of *C. stenocephalus stenocephalus* by some authors (Březina 1999; Lorenz 2005), is considered to be a “*natio*” by Breuning (1932-1937) and a valid “weak” subspecies by Deuve (1994; 2004).

For their close geographic vicariance and their clinal morphological variation along the Atlantic Moroccan coast (from stocky, tenebrionid-like Northern forms to more elongate, cychrized Southern forms), these taxa are considered as belonging to a single species by some authors. Lapouge (1936) ascribed a single polytypic species to *Cathoplius (Calosoma asperatum* Dejean, 1826) and his opinion is still maintained in some recent catalogues (Březina 1999; Bousquet *et al.* 2003; Lorenz 2005).

The systematic position of the Subgenus *Cathoplius* remains complicated and controversial. Lapouge (1930), who first proposed an accurate phylogenic systematics of the Genus *Carabus*, placed *Cathoplius* within his “Psilogoniens”, close to several other subgenera (some regarded as synonyms in recent phylogenies, some others totally displaced). He considered *Cathoplius* close to *Mesocarabus (dufourii* Dejean, 1829) and *Eurycarabus (famini lucasi* Gaubil, 1849) simply by observing the elytral sculpture (and presumably also by considering their geographic proximity). He reported the combination of some very peculiar characters of these taxa, including the lack of gular setae, the presence of an anterior collar in the prothorax, only three tarsomers with ventral adhesive hairs in anterior tarsi of males, protibiae with a strong anterior apophysis (typical of fossorial, sandy dweller species), and some characters of male genitalia. Finally, he concluded that representatives of the Subgenus *Cathoplius* probably originate from a lineage close to “Multistriés”.

Breuning (1932-1937), who like Lapouge was unaware of the larval morphology of *Cathoplius*, subdivided Genus *Carabus* into two main groups: Carabi *brevimandibulares* (with a quadricuspid larval morphology *sensu* Lapouge) and Carabi *longimandibulares* (corresponding to the rostrilabrum larval type *sensu* Lapouge, or to the Neocarabi of Bengtsson). In his taxonomic treatment, Breuning placed *Cathoplius* into *brevimandibulares*, as the last Subgenus, close to *Eurycarabus* Géhin, 1885, likely having been influenced by Lapouge’s descriptions.

In more recent contributions, the Subgenus *Cathoplius* has been placed in different placements. Deuve (1991) based his taxonomic approach on the characters of endophallus emphasized by Ishikawa, and placed *Cathoplius* in a basal position within Multistriati of Lapouge *sensu* Ishikawa (1978), which include several subgenera previously assigned to *brevimandibulares* by Breuning (1932-1937). Later, the same author (Deuve 1994), established a new group, Lobifera (= Multistriati *sensu* Ishikawa, 1978, nec Reitter, 1896, nec Lapouge, 1930), which includes several *brevimandibulares sensu* Breuning, and placed *Cathoplius* in Lobifera between *Mesocarabus* Thomson, 1875 and *Oxycarabus* Semenov, 1898. Březina (1999) placed *Cathoplius* within the Procrustimorphi of Imura (1996). Finally, Deuve (2004) placed *Cathoplius* as the only Subgenus of the section Cathopliogenici (= Cathopliigenici of Imura, 2002), within the Metacarabi of Bengtsson (1927). The position within Cathopliogenici, as a sister group of the Neocarabi of Bengtsson (1927), was confirmed and maintained in a subsequent contribution based on the molecular phylogeny of the Genus *Carabus* (Deuve *et al.* 2012).

In the present contribution, data on the life-cycle and pre-imaginal morphology of *Cathoplius* sampled in different Moroccan areas are given. These data bring new information to some of the previously highlighted taxonomic and phylogenetic questions.

Material and methods

Our field observations on ground beetles of Subgenus *Cathoplius* are the results of many surveys carried out during several years. Specifically, one of the authors (C. G.) has sampled specimens of different *Cathoplius* populations in 1992 (March-April), 1994 (May), 1999 (December), 2000 (January), 2006 (January, February-March, April), 2008 (March; November, with E. B.), 2010 (January, December), 2012 (April, with E. B.), 2013 (May, with E.B.) and 2014 (April, with A.C.).

Data reported in the present work are the result of *Cathoplius* couples breeding, sampled as follows:

1♂ - 1♀ *Carabus (Cathoplius) asperatus* (Dejean, 1826)

– Morocco, (Sidi Bennour) Oualidia, 45 m a.s.l., 14 November 2008 - C. Ghittino & E. Busato legit.

1♂ - 1♀ *C. (Cathoplius) stenocephalus stenocephalus* Lucas, 1866

– Morocco, (Essaouira) Essaouira, Sidi Kaouki, 2 m a.s.l., 12 November 2008 - C. Ghittino & E. Busato legit.

2♂♂ - 2♀♀ *C. (Cathoplius) stenocephalus susicus* Antoine, 1941

– Morocco, (Tiznit) Aglou Plage, 25 m a.s.l., 10 November 2008 - C. Ghittino & E. Busato legit.

1♂ - 1♀ *C. (Cathoplius) stenocephalus ifniensis* Zarco, 1941

– Morocco, (Sidi Ifni) Sidi Ifni, 10 m a.s.l., 8 November 2008 - C. Ghittino & E. Busato legit.

3♂♂ - 3♀♀ *(Cathoplius) stenocephalus aliai* Escalera, 1944

– Morocco, (Tan-Tan) Tan-Tan, 90 m a.s.l., 18 December 2010 – C. Ghittino legit.

In addition to pure breeding of adults of the different *Cathoplius* species and subspecies, hybridization trials between *C. asperatus* and *C. stenocephalus stenocephalus*, *C. stenocephalus ifniensis* and *C. stenocephalus susicus*, and *C. stenocephalus ifniensis* and *C. stenocephalus aliai*, were also carried out.

Adults and pre-imaginal stages were bred at DISAFA laboratories in Torino, Italy. The breeding methodology used was basically that reported by Malausa (1977), to which some adjustments were applied.

For each taxon, one to three adult couples were bred, by placing them into a 35 x 23 x 13 (width x length x height) cm transparent terrarium, with a perforated top for aeration. A 6 cm substrate, composed of a mixture of sand (70%) and argillaceous soil (30%), was placed on the bottom of each terrarium. The substrate was kept moist by periodic spraying with water. One third of the substrate surface was covered with a layer of moss. Breeding of couples was carried out at a temperature of $21\pm 1^\circ\text{C}$. Adults were fed mainly live snails belonging to the species *Theba pisana* (O.F. Müller, 1774), and occasionally with small specimens of *Eobania vermiculata* (O.F. Müller, 1774).

Larvae, bred individually to avoid cannibalism problems, were maintained in cylindrical transparent plastic containers (13 cm height, 10 cm in diameter) at the same temperature as terrariums for adults, and were fed with live *T. pisana* of the appropriate size.

Data were collected from the observation of 100 individuals per taxon. Mean duration of the larval and pupal stages of the five studied taxa, as well as the interval of time between emergence from the pupa and rising to the surface, were compared through Kruskal-Wallis non parametric tests. When a significant difference was seen, Dunn's test for multiple comparison was applied to the different variables, to compare pairs of data. Mean values of *frontoclypeolabrum* length and width ratio of first, second and third instars of the studied taxa were compared through one-way analysis of variance (ANOVA). In the case of significant differences, Tukey's test for multiple comparisons was applied to separate means.

Specimens used in this study (larvae, pupae, adults) are conserved dry or under alcohol in authors' collections. Some larvae of different instars were placed on a plastozote base, then dipped in 70% alcohol and drawn. The total number of laid eggs was evaluated by defect and is ascribed to the number of hatched larvae, being impossible to count the exact number of eggs present in the substrate without damaging them. For larval structure general terminology we referred to Lapouge (1905-08), Böving (1911), Jeannel (1920), Casale *et al.* (1982), Lawrence (1991) and partly to Arndt & Makarov (2003). Recording of primary setae and pores followed the system of Bousquet and Goulet (1984), Bousquet (1985; 2010) and Makarov (1993).

Acronyms.

L: overall length of adults, from apex of mandibles to apex of elytra, measured along the suture (mm).

l/w: length/width ratio of *frontoclypeolabrum* in larvae.

a/M: antenna/mandible length ratio in larvae.

m/M: maxilla/mandible length ratio in larvae.

PL/PW: ratio between length of pronotum, as linear distance from anterior to basal margin measured along the midline, and maximum width of pronotum in adults.

Results

Adult behavior and oviposition

Adults, fed with *T. pisana* and occasionally with *E. vermiculata*, were found to be very voracious (Fig. 1). Due to their narrow and elongate head, that can be considerably everted from the thorax by folding to 90° , they were able to penetrate inside the shell of their prey, even though this was retracted in-depth. Once the mollusk was secured, it was pulled to extract it from the shell. Each

meal lasted for an average of approximately two hours. During a meal, if disturbed by other individuals or by the breeder's maintenance activities, adults were grasping the snail at the hedge of the operculum and were taking it under a shelter for subsequent consumption.

Males were particularly active only during the night and early morning. Although females fed throughout the day, they were also more active during the night and early morning. A few hours after eating a sufficient number of snails, adults began to mate and, after 1-4 days, egg laying took place. Mating occurred throughout the whole oviposition period. Males were frequently observed mating with females while the females were eating (Fig. 2).

After mating, the females, using their mandibles and legs, began digging an oblique gallery in the soil. Then they inserted their abdomen into the gallery, covering themselves until the thorax was entirely buried (Fig. 3). Inside the gallery, the females laid several eggs at a variable depth (from 1 to 40 mm) and at a regular distance between eggs. In rare occasions, eggs were found under the moss layer (Fig. 4). Larger females were able to lay their eggs deeper in the substrate. When laying was complete, the females sealed the gallery and the oviposition location was marked by a depression in the substrate.

The oviposition of a *C. stenocephalus stenocephalus* female close to the terrarium-side allowed us to measure the distance between eggs, a distance corresponding to about 14 to 20 mm. The egg cell was round in shape, with a diameter of 5 mm. When oviposition ceased, females buried themselves at the maximum depth in the terrariums (6 cm) and fell into diapause. The total number of eggs laid by each female and the laying frequency is reported in Table 1.

TABLE 1. Total number of laid eggs per female, oviposition period and oviposition rate.

TAXON	♀♀	TOTAL NO. OF LAID EGGS	OVIPOSITION PERIOD	OVIPOSITION RATE (EGGS/DAY)
<i>C. asperatus</i> (Dejean, 1826)	1 st ♀	241	from 30/11/2008 to 23/01/2009	4.46
<i>C. stenocephalus stenocephalus</i> Lucas, 1866	1 st ♀	288	from 30/11/2008 to 18/01/2009	5.88
<i>C. stenocephalus susicus</i> Antoine, 1941	1 st ♀	511	from 30/11/2008 to 10/01/2009	12.46
	2 nd ♀	423	from 30/11/2008 to 10/03/2009	4.23
<i>C. stenocephalus ifniensis</i> Zarco, 1941	1 st ♀	342	from 30/11/2008 to 12/01/2009	7.95
<i>C. stenocephalus aliai</i> Escalera, 1944	1 st ♀	302	from 28/12/2010 to 02/04/2011	3.51
	2 nd ♀	261	from 30/11/2011 to 01/03/2012	2.87
	3 rd ♀	289	from 30/11/2011 to 22/02/2012	3.44

At the end of the late autumn-winter breeding period, which lasted for approximately 50 to 100 days depending on the *Cathoplius* taxon, adults of the parental generation buried themselves and fell into diapause for 1 to 2 months. After this period, in the late winter-spring, they became active again and bred for a second time, but the number of larvae generated was found to be lower (1/3 less compared to the first breeding period).

An exception to this was represented by the desert dwelling taxon *C. stenocephalus aliai*, whose adults of the parental generation, even with optimal temperature and humidity conditions, did not appear to breed a second time and, if they did, a reduced number of scarcely viable larvae was generated. In *C. stenocephalus aliai*, all adults died following the breeding period.

In *C. asperatus* and in the other *C. stenocephalus* subspecies, after completing integument sclerification (17-35 days) and after a short diapause (20-30 days), adults of the first generation emerged in winter (F1) started breeding simultaneously to those of the parental generation, producing a second spring progeny (F2), that was numerically inferior to the one of the winter

generation. Adults of the parental generation, as well as those of the first winter (F1) and second spring (F2) generations, then underwent a summer diapause. Neo-emerged adults fed until complete sclerification and fell into diapause without reproducing. Breeding took place during the following late autumn-winter. In laboratory conditions, adult specimens survived for about 1-1.5 years and died during the second winter.

Egg morphology and embryonic development

When laid, eggs of *Carabus* of the Subgenus *Cathoplius* (Fig. 4) were diaphanous white in color and measured 4.5-5 x 1.5 mm (differences between *C. asperatus* and *C. stenocephalus* eggs are not significant). With time, the eggs gradually became a clear yellow color. Their size increased considerably during embryonic development, reaching 5.5 x 2.5 mm at complete development. At $21\pm 1^{\circ}\text{C}$, the embryonic development in all taxa was completed in about 14-15 days, with the exception of *C. stenocephalus susicus*, where it was achieved in 13 days.



FIGURES 1-4. *Carabus stenocephalus susicus* adult preying a small *Eobania vermiculata* (1); mating adults of *C. stenocephalus aliai* (2); *C. stenocephalus ifniensis* female while laying (3); *C. asperatus* eggs laid on moss (4).

Pre-imaginal development and larval behavior

Newborn larvae of the different species and subspecies of *Cathoplius* measured 9.2-12.0 mm (*C. asperatus*), 8.8-12.5 mm (*C. stenocephalus stenocephalus*), 10.0-12.5 mm (*C. stenocephalus susicus*), 11.0-14.3 mm (*C. stenocephalus ifniensis*) and 9.5-12.0 mm (*C. stenocephalus aliai*) in length, respectively. After hatching, larvae remained in the egg cell for about one day to complete sclerification, then they came up to the surface. Once on the surface, larvae ran about frenetically, climbing on any obstacle in their path while searching for food.

A particular preying behavior was noticed with a *Cathoplius* larva upon finding an everted snail. It moved closer to the snail, almost touching it with its mandibles. Then, it repeatedly struck the snail head through its urogomphi, raising and moving forward the distal abdominal segments (the so called “scorpion move”). In this way, the snail was forced to draw into the shell, becoming an easy prey to overcome. Subsequently, the larva penetrated inside the shell by keeping its ventral side of the body adhering to the shell walls.

Larvae were found to be very aggressive and, despite their small size, they were able to kill large *Theba* snails; only sporadically, were they found dying of suffocation by mollusk mucus. Duration of meals was proportional to snail size: if the snail was large, a single meal was sufficient for the completion of the first instar period. Some days before each ecdysis, the larvae were digging a pit under a shelter (Fig. 5). Sometimes, and more frequently prior the second ecdysis, the larvae dug a cell into the soil (Fig. 6). The larvae then remained steel, lying on their back until the time of ecdysis. Often, ecdysis took place inside the snail shell (Fig. 7), where exuviae were normally found (Fig. 8). Ecdysis was very fast, taking 24 to 36 hours. After a short period of time during which the integument sclerification occurred, the larvae began feeding again.

Minimum and maximum length of the three larval instars are shown in Table 2 (measures are approximate, since total length of the larva varies according to the quantity of feed ingested).

TABLE 2. Minimum and maximum length of the three larval instars of the species and subspecies of Subgenus *Cathoplius*.

TAXON	1 st INSTAR LARVA MINIMUM AND MAXIMUM LENGTH (mm)	2 nd INSTAR LARVA MINIMUM AND MAXIMUM LENGTH (mm)	3 rd INSTAR LARVA MINIMUM AND MAXIMUM LENGTH (mm)
<i>C. asperatus</i> (Dejean, 1826)	9.2÷13.9	13.0÷20.0	19.2÷29.0
<i>C. stenocephalus stenocephalus</i> Lucas, 1866	8.8÷14.0	13.4÷20.4	20.1÷29.8
<i>C. stenocephalus susicus</i> Antoine, 1941	10.0÷14.3	14.0÷22.0	20.0÷32.0
<i>C. stenocephalus ifniensis</i> Zarco, 1941	11.0÷18.0	17.0÷25.0	23.0÷35.0
<i>C. stenocephalus aliai</i> Escalera, 1944	9.5÷16.5	16.0÷21.5	22.0÷30.0

When disturbed, *Cathoplius* larvae demonstrated a fear response: they contracted their body, arched the thorax, raised the head and the abdominal urite bearing the urogomphi, and regurgitated a drop of liquid of dark brown color on their head and part of their thorax. If larvae were touched on the back, they rapidly raised the extremities of their body, bending with a “U” shape, and striking vigorously the source of the stimulus with both the urogomphi and mandibles.

At the end of the third instar period, the mature larva stopped feeding and started digging a large cell for pupating (Fig. 9), in so doing leaving a small mound of earth on the substrate surface. Inside the cell, the larva occupied from 1/3 to 2/3 of the cell length. Occasionally, a pupal instar occupied a pit under the surface shelter (Fig. 10) but in this case, after emergence from the pupa, the adult was found to be malformed.

After emergence (Figs 11-14), adults remained in the pupal cell for a variable period of time (2.5-5 days) and they rose to the surface only when their integument was solid enough. Just after

emergence, while sclerification of the integument was taking place, adults changed their position various times inside the pupal cell, either by lying on their abdomen, or on their side or back. Once on the surface, adults began to prey on snails until their total hardening which was completed in approximately 17-35 days, depending on the taxon. Afterwards, adults buried themselves and fell into diapause. The duration of larval development, from egg hatching to digging of pupal cell, and from prepupal and pupal period to imago, of the different *Cathoplius* species and subspecies kept under laboratory conditions (with *ad libitum* feeding) is reported in Table 3. Observations were carried out on 100 individuals per bred taxon.



FIGURES 5-10. *Carabus stenocephalus susicus* 3rd instar larva that underwent ecdysis in a cell dug under a shelter (5); *C. stenocephalus susicus* 3rd instar larva after ecdysis in a cell dug in the soil, visible in transparency through the breeding container (6); *C. stenocephalus susicus* 3rd instar larva that underwent ecdysis inside a *Theba* snail: exuviae have been pushed externally (7); exuviae of a *C. stenocephalus stenocephalus* 2nd instar larva inside a preyed snail (8); *C. asperatus* pupa inside a cell dug at a depth of 6.5 cm (9); *C. asperatus* pupa inside a cell dug under a surface shelter (10).

Larval development analysis showed a shorter duration of the first instar period for *C. stenocephalus aliai* (6 days in average), followed by *C. stenocephalus susicus* (6.8 days) and then by the other three taxa (7-7.3 days). The duration of the second instar period was found to be shorter in *C. stenocephalus susicus* (6.7 days), while no significant differences were noticed between *C. asperatus*, *C. stenocephalus stenocephalus*, *C. stenocephalus ifniensis* and *C. stenocephalus aliai*

(7.7-8 days). The duration of the third instar period was also shorter in *C. stenocephalus susicus* (13.7 days), followed by *C. stenocephalus aliai* (15.4 days) and then by the remaining taxa (17.3-18.1 days).



FIGURES 11-14. Partly pigmented pupa close to emergence (11); Pigmentation phases in a neo-emerged *Carabus stenocephalus stenocephalus* male: right after emergence (12); after two hours from emergence (13); at almost completed pigmentation (14).

TABLE 3. Duration of larval and pupal development and duration of the rising to the surface period in the species and subspecies of Subgenus *Cathoplius*. Means followed by different letters in the same column are significantly different from each other (Dunn's Test, $P < 0.05$).

TAXON	1 st INSTAR (PRE-ECYDYSIS PERIOD) (MEAN DAYS \pm SE)	2 nd INSTAR (PRE-ECYDYSIS PERIOD) (MEAN DAYS \pm SE)	3 rd INSTAR (PRE-PUPAL PERIOD) (MEAN DAYS \pm SE)	PUPA (MEAN DAYS \pm SE)	PERIOD BETWEEN EMERGENCE FROM THE PUPA AND RISING TO THE SURFACE OF IMAGINES (MEAN DAYS \pm SE)
<i>C. asperatus</i> (Dejean, 1826)	6.980 \pm 0.200 A (1.857 \pm 0.108) a	7.737 \pm 0.229 A (2.451 \pm 0.152) a	17.746 \pm 0.467 A (10.683 \pm 0.399) a	16.862 \pm 0.178 BC	5.121 \pm 0.123 A
<i>C. stenocephalus stenocephalus</i> Lucas, 1866	7.196 \pm 0.230 A (1.920 \pm 0.0987) a	7.722 \pm 0.272 AC (2.393 \pm 0.149) a	18.055 \pm 0.296 A (10.341 \pm 0.138) a	17.225 \pm 0.162 BC	5.128 \pm 0.256 A

<i>C. stenocephalus susicus</i> Antoine, 1941	6.790±0.206 AC (2.063±0.143) a	6.701±0.227 BC (2.464±0.238) a	13.705±0.241 C (8.010±0.157) b	16.737±0.204 C	5.069±0.096 A
<i>C. stenocephalus ifniensis</i> Zarco, 1941	7.348±0.267 A (1.909±0.0909) a	7.693±0.272 A (2.500±0.174) a	17.266±0.276 A (9.586±0.118) a	17.641±0.137 B	5.283±0.107 A
<i>C. stenocephalus aliai</i> Escalera, 1944	6.020±0.077 BC (1.920±0.114) a	8.020±0.077 A (2.464±0.167) a	15.370±0.145 B (6.600±0.067) c	22.600±0.063 A	2.480±0.054 B

In contrast to larval development, the duration of the pupal instar was found to be longer in *C. stenocephalus aliai* (22.6 days in average) as compared to all other taxa (16.7-17.6 days).

Lastly, the time between emergence from the pupa and rising to the surface of imagines was shorter in *C. stenocephalus aliai* (2.5 days in average) in comparison with the other taxa (about 5 days).

Morphological characters of larvae

Due to the marked similarity between the studied taxa, description of larval characters will be done jointly and differences will then be highlighted on a case by case basis.

Larvae are of rostrilabre tenuirostrum type (according to Lapouge 1905-08), highly sclerotized, uniformly black in color, and morphologically matching those typical of helicofagous species within the Genus *Carabus* Linnaeus, 1758 (Figs. 15-19).

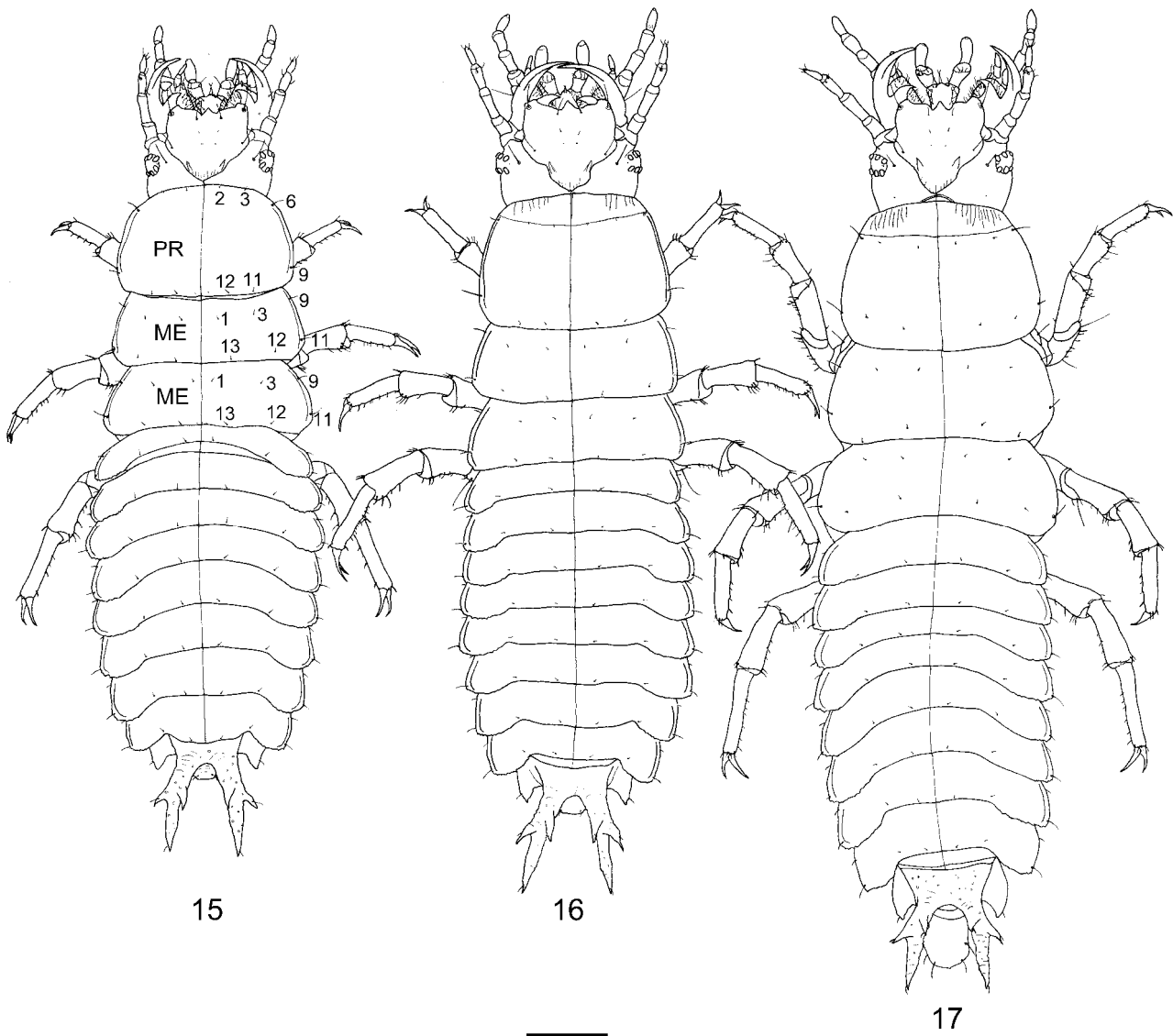
Microsculpture: mouth parts, frontal and parietal areas of head, and legs possess meshes with isodiametric reticulation, while tergites and urogomphi have isodiametric to transversal reticulations, and tergite IX and sternites have reticulate to punctuate reticulations.

Head is subquadrate (Figs. 15-19). The metopical suture (“coronal”) is very short. Frontal sutures are well visible and deeply sinuous. In *C. asperatus* the *frontoclypeolabrum* is significantly different from that of the other *Cathoplius* taxa: it is usually a little wider than long in first and second instars, and barely longer than wide in the third instar. In contrast, in *C. stenocephalus* the first instar *frontoclypeolabrum* is barely longer than wide, while it becomes progressively wider than long in the subsequent instars. Length/width (l/w) ratios of the *frontoclypeolabrum* of the three larval instars of the species and subspecies of Subgenus *Cathoplius* are reported in Table 4. Eye area is moderately prominent, provided with six stemmata and three setae (PA₇, PA₉, PA₁₃). The anterior margin of the *frontoclypeolabrum* (“nasal”) (Figs. 20-25, 37-42, 54-59, 71-76, 88-93) is markedly trilobate. *Hypodon* is not visible from the dorsal side, but only from the ventral side. The anterior margin is almost perpendicular to the body axis, with the exception of an area contiguous to the median lobe, where a more or less rounded cove is evident. In the normal position, the *frontoclypeolabrum* has five pairs of dorsal setae: a long one (FR₇), two medium long ones (FR₂, FR₅), a very short one (FR₄), and one similar to pores (FR₃). The median lobe is more or less rounded, with a small axial prominence, which is more or less evident depending on the specimen observed. In the first instar, lobes profile is marked and pointed, and it becomes more rounded in the second and third instars. In all instars, the median lobe is usually at a lower level compared to the level of lateral lobes. Sporadically, in some specimens, it is on the same level. In the proximal part of the *frontoclypeolabrum* of the first instar larvae, the *ruptor ovi* is present: it is formed by two spinulae, one on each side, which are anteriorly oriented.

TABLE 4. Length/width (l/w) ratios of the *frontoclypeolabrum* of the three larval instars of the species and subspecies of Subgenus *Cathoplius*. Means followed by different letters in the same column are significantly different from each other (Tukey’s Test, P<0.05).

TAXON	1 st INSTAR		2 nd INSTAR		3 rd INSTAR	
	no.	l/w (m ± SE)	no.	l/w (m ± SE)	no.	l/w (m ± SE)
<i>C. asperatus</i> (Dejean, 1826)	10	0.911±0.00505 c	10	0.958±0.00558 c	10	1.045±0.00635 a
<i>C. stenocephalus stenocephalus</i> Lucas, 1866	10	1.079±0.00562 ab	10	0.978±0.00360 bc	10	0.935±0.00609 c
<i>C. stenocephalus susicus</i> Antoine, 1941	10	1.075±0.00590 b	10	1.001±0.00578 ab	10	0.944±0.00685 c
<i>C. stenocephalus ifniensis</i> Zarco, 1941	10	1.100±0.00614 a	10	1.017±0.00532 a	10	0.969±0.00612 b
<i>C. stenocephalus aliai</i> Escalera, 1944	10	1.083±0.00481 ab	10	0.979±0.00786 bc	2	0.903±0.00547 c

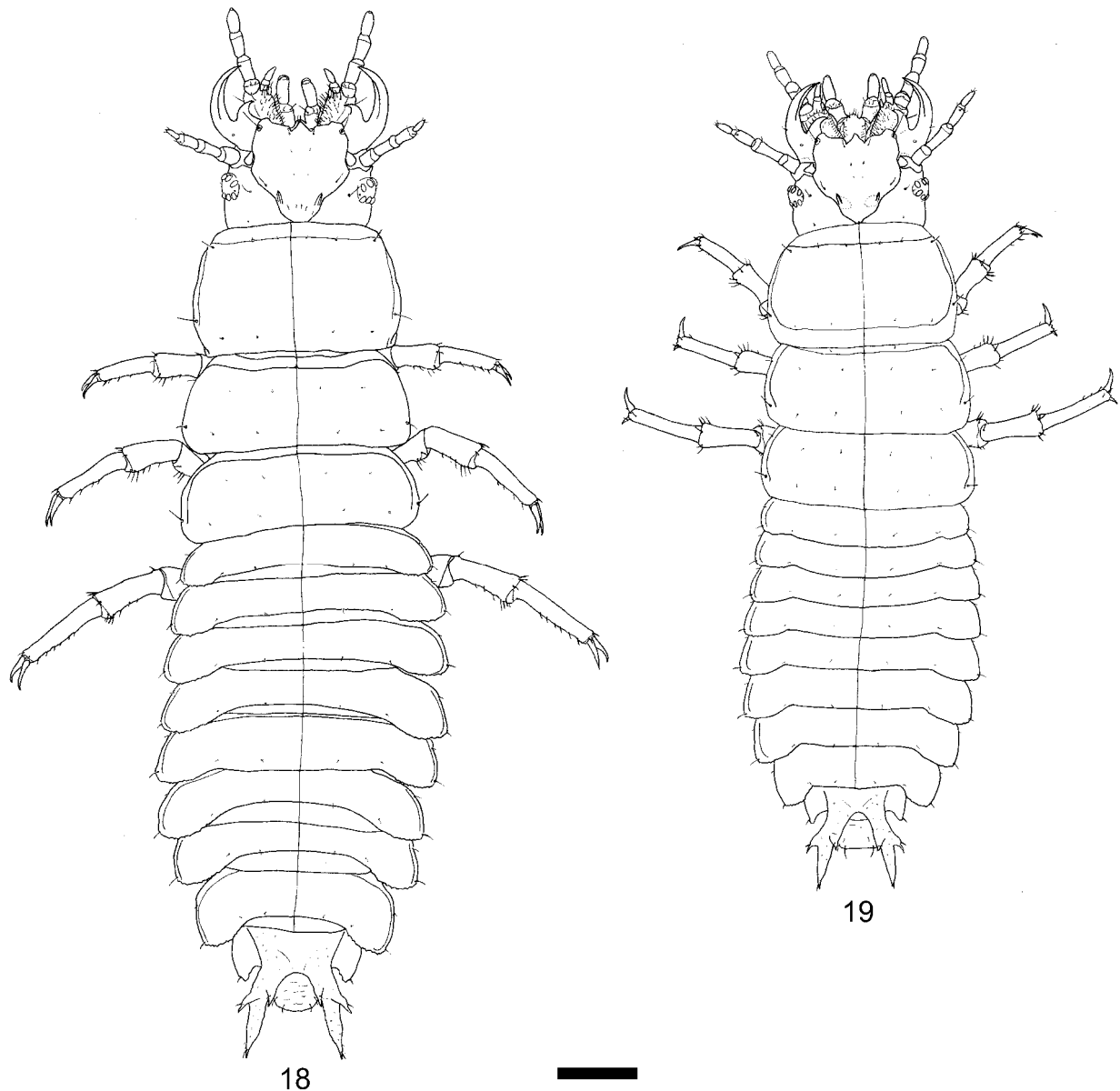
Antennae (Figs. 26-28, 43-45, 60-62, 77-79, 94-96) have only primary setae (“ancestral” setae *sensu* Arndt *et al.* 1994) (AN₁, AN₂, AN₃, AN₄, AN₅, AN₆, AN₇), and are slightly longer than mandibles. The antenna/mandible (a/M) length ratio of a first instar specimen taken as an example for each taxon is 1.08 (*C. asperatus*), 1.15 (*C. stenocephalus stenocephalus*), 1.09 (*C. stenocephalus susicus*), 1.17 (*C. stenocephalus ifniensis*) and 1.24 (*C. stenocephalus aliai*). The first segment is subcylindrical. The second segment is similar, narrower and slightly dilated distally, one and a half as long as the first one, slightly shorter than the third and slightly longer than the fourth. The third segment is also subcylindrical, slightly dilated apically and provided with a domed sensillum, lateral to the insertion point of the fourth cylindroconical article. Distally, the fourth segment is provided with some small sensilla located among the setae (AN₄, AN₅, AN₇). In *C. asperatus*, antennae are clearly shorter than in *C. stenocephalus* (in the broad sense), despite having the same length ratios of segments.



FIGURES 15-17. Dorsal aspect of the first instar larva of: *Carabus asperatus* (15); *C. stenocephalus stenocephalus* (16); *C. stenocephalus susicus* (17). Habitus (Scale: 1 mm).

Mandibles (Figs. 29, 46, 63, 80, 97) are falciform, robust, with a robust sharpened and curved retinacle at the base of which there is a tuft of setae (*penicillium*). The internal margin is smooth. At mid-length on the external margin the MN_1 seta is present, while the MN_2 seta is absent.

Maxillae (Figs. 30-31, 47-48, 64-65, 81-82, 98-99) are longer than mandibles. The maxilla/mandible (m/M) length ratio of a first instar specimen taken as an example for each taxon is 1.46 (*C. asperatus*), 1.52 (*C. stenocephalus stenocephalus*), 1.46 (*C. stenocephalus susicus*), 1.36 (*C. stenocephalus ifniensis*) and 1.63 (*C. stenocephalus aliai*). The stipe is nearly half as wide as long and provided with several setae on the internal edge of the dorsal side (gMX). On the maxillary palps, which are composed of four articles, the first article is subquadrate with rounded edges, the second and third are cylindroconic and clearly more elongated and the fourth is cylindroconic as long as the second one and a little longer than the third. The first article has a medium-length seta (MX_{10}) on the ventral side and depending on the specimen observed, but



FIGURES 18-19. Dorsal aspect of the first instar larva of: *Carabus stenocephalus ifniensis* (18); *C. stenocephalus aliai* (19). Habitus (Scale: 1 mm).

independently from the taxon, has from two to four additional setae on the dorsal side. The galea has two articles, the first being slightly narrower in the distal part and clearly shorter than the second which has a very small seta (MX₇) on the ventral side. The lacinia is cylindroconical with an apical seta (MX₆).

The *labium* (Figs. 32-33, 49-50, 66-67, 83-84, 100-101) has two pairs of ventral setae (LA₁, LA₂) and several dorsal setae (LA₄, LA₅, gLA₃) and the ligula has two setae (LA₆). The labial palps are articulated with the sides of the *labium* and are formed by two subcylindrical palpomeres, the basal one being slightly enlarged distally and a little shorter than the second that is dorsally supplied with four to five setae on the distal third (gLA_b). The apical palpomere is slightly bilobate at the apex, with apical palpares of the same size.

The thorax (Figs. 15-19) has a reduced chaetotaxy: PR₄, PR₅, PR₈, PR₁₀ setae are absent and PR₁₃, PR₁₄ are very short or similar to pores. ME₂, ME₁₀ on meso- and metanotum are absent.

Urotergites (Figs. 34, 51, 68, 85, 102) have depressed lateral margins forming broad posterior lobes that are slightly denticulated along their internal margin. All urotergites have nine setae, seven of which are very short and very fine (TE_1 , TE_2 , TE_3 , TE_5 , TE_{10} , TE_{11} , TE_7). In some specimens setae are absent or similar to pores (TE_1 , TE_5 , TE_7 , in particular). The remaining two setae are very robust and are placed along the external margin with one of medium-length (TE_9) and the other less than half as long as the first (TE_7).

Urite IX (Figs. 35, 52, 69, 86, 103) has narrower and more angled lateral-posterior lobes that may have smoothed extremities each provided with a seta on the external margin of the apical third (UR_2). Occasionally on some *C. asperatus* specimens, a second rear seta positioned on the external margin can be observed.

Urogomphi are conical, not articulated and robust, curved upside and parallel or more frequently divergent depending on the specimen observed but independently from the taxon. They have a rough integument and are provided with a sharp apex. The upper spina is analogous or slightly less developed than the lateral one and bears a fine and short seta (UR_4). On the lateral spine a short and very robust seta (UR_5) is present.

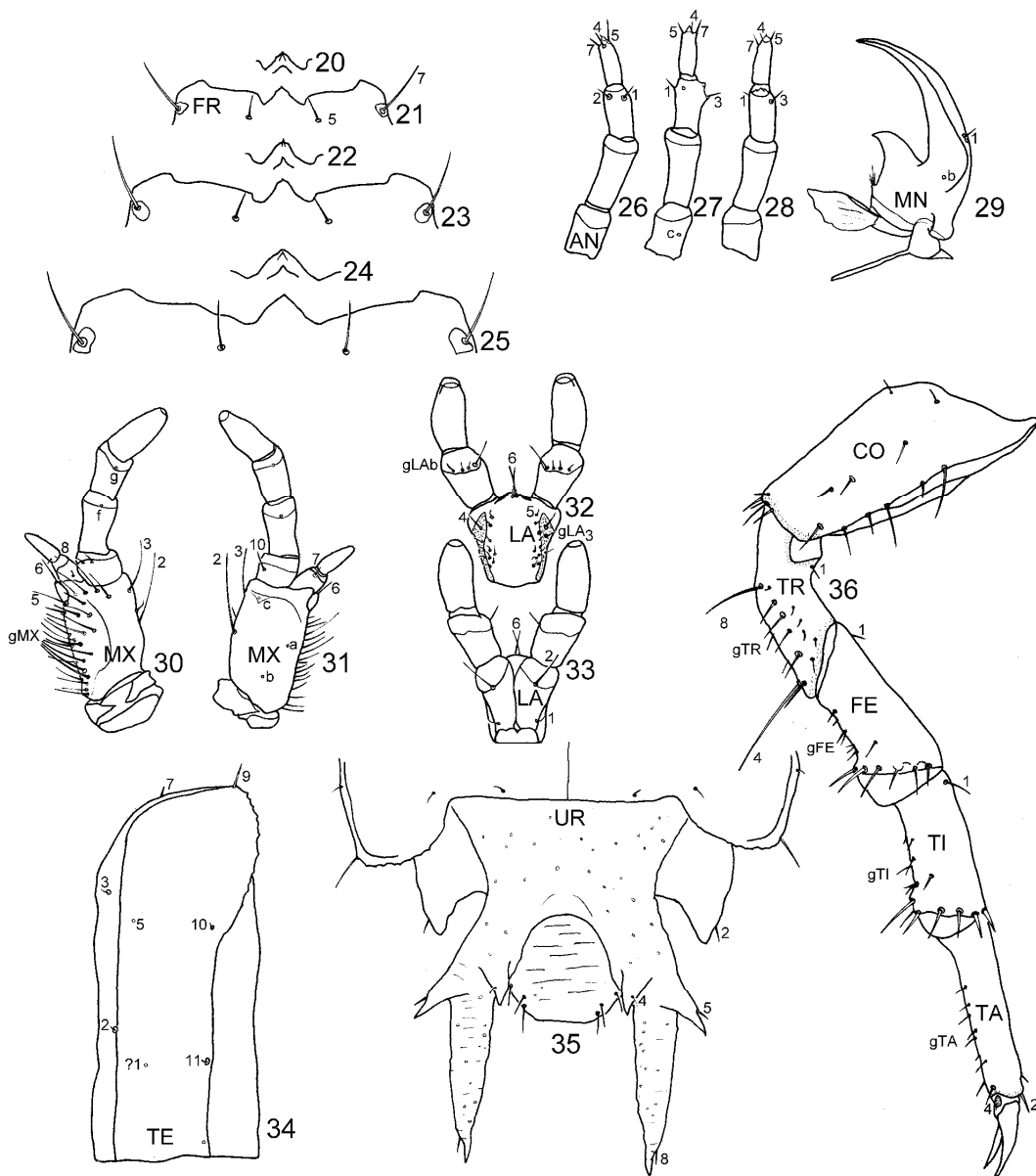
Legs (Figs. 36, 53, 70, 87, 104) are quite robust and elongate; trochanter, femur, tibia and tarsus have spines in longitudinal rows. The chaetotaxy is in agreement with the model proposed by Makarov (1993). The morphometric ratios of the left metathoracic leg of a first instar larva taken as an example for each taxon are reported in Table 5.

TABLE 5. Morphometric ratios of the left metathoracic leg in a first instar larva of the different species and subspecies of Subgenus *Cathoplius* (C: coxa; T: trochanter; F: femur; t: tibia; ta: tarsus).

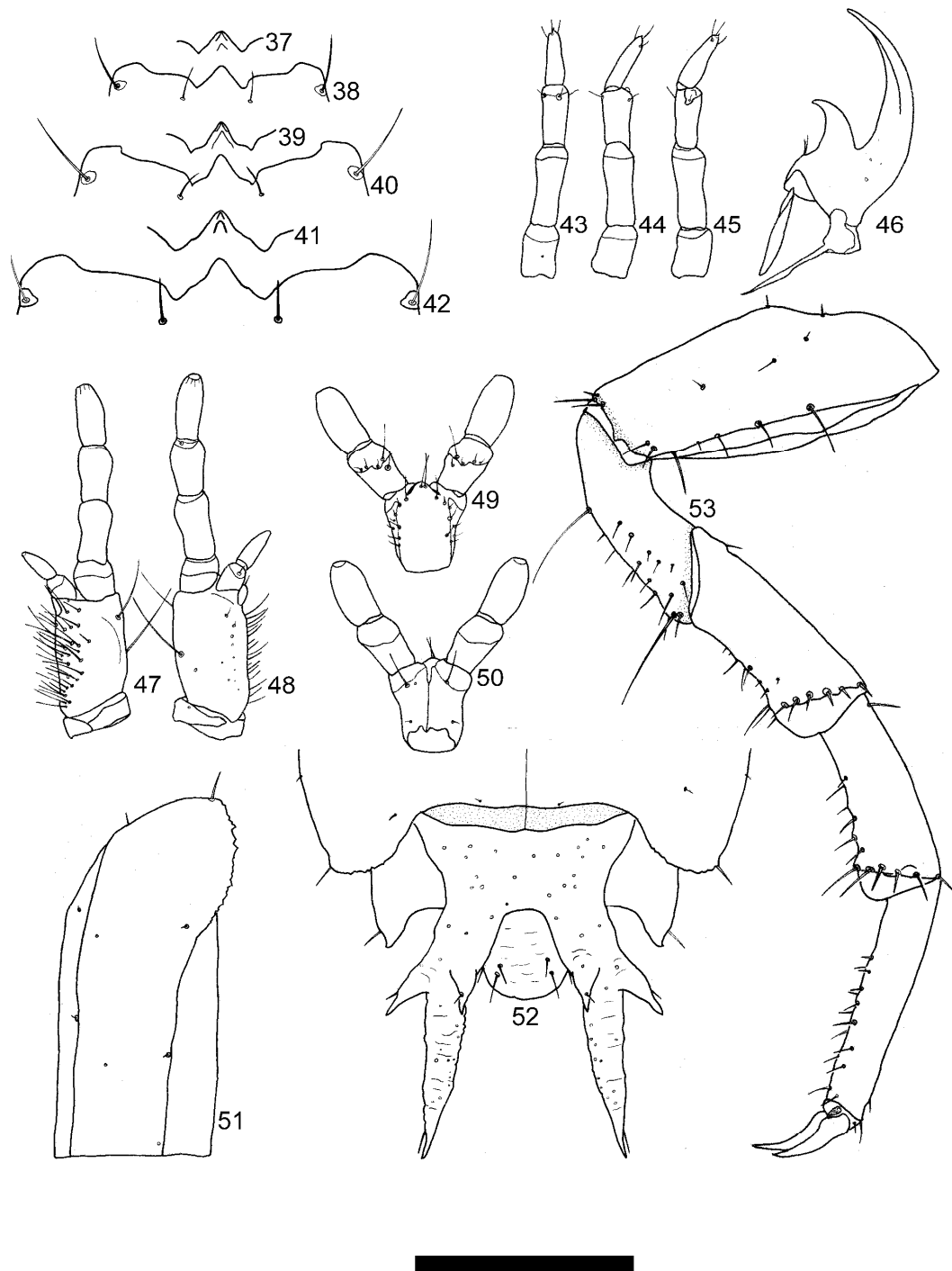
TAXON	T/C	F/C	t/C	ta/C
<i>C. asperatus</i> (Dejean, 1826)	0.74	0.70	0.57	0.70
<i>C. stenocephalus stenocephalus</i> Lucas, 1866	0.69	0.65	0.57	0.75
<i>C. stenocephalus susicus</i> Antoine, 1941	0.70	0.74	0.63	0.76
<i>C. stenocephalus ifniensis</i> Zarco, 1941	0.77	0.75	0.57	0.73
<i>C. stenocephalus aliai</i> Escalera, 1944	0.68	0.70	0.56	0.77

Morphological characters of pupae

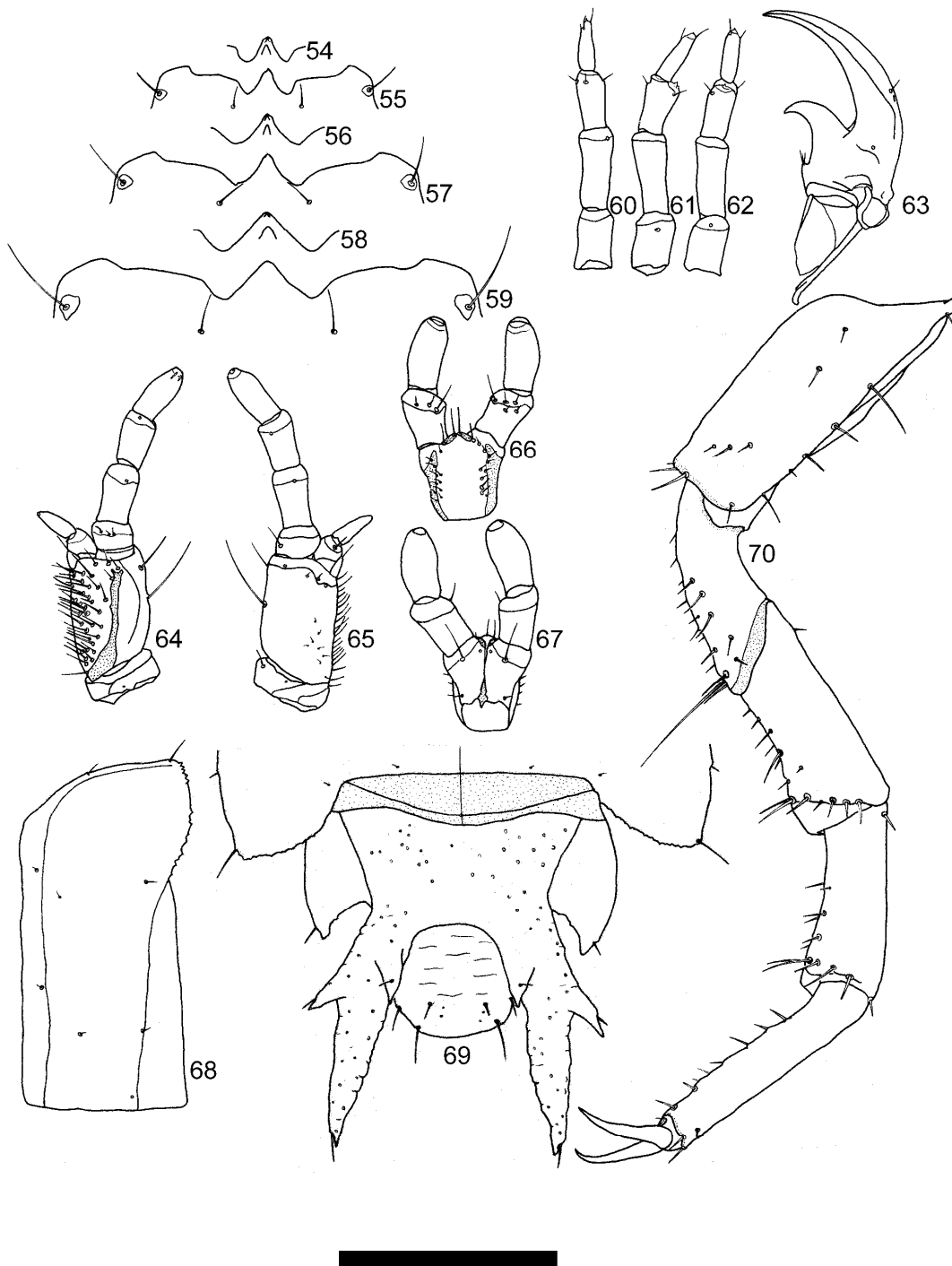
Pupae of the various taxa belonging to Subgenus *Cathoplius* (Figs. 105-111) reflect the general aspect of adults: the pupa of *C. asperatus* is more stocky with a wider thoracic area while the thoracic area gets progressively narrower and more elongated by passing from Northern to Southern *C. stenocephalus* subspecies. The pupa of *C. stenocephalus ifniensis* is the largest in size.



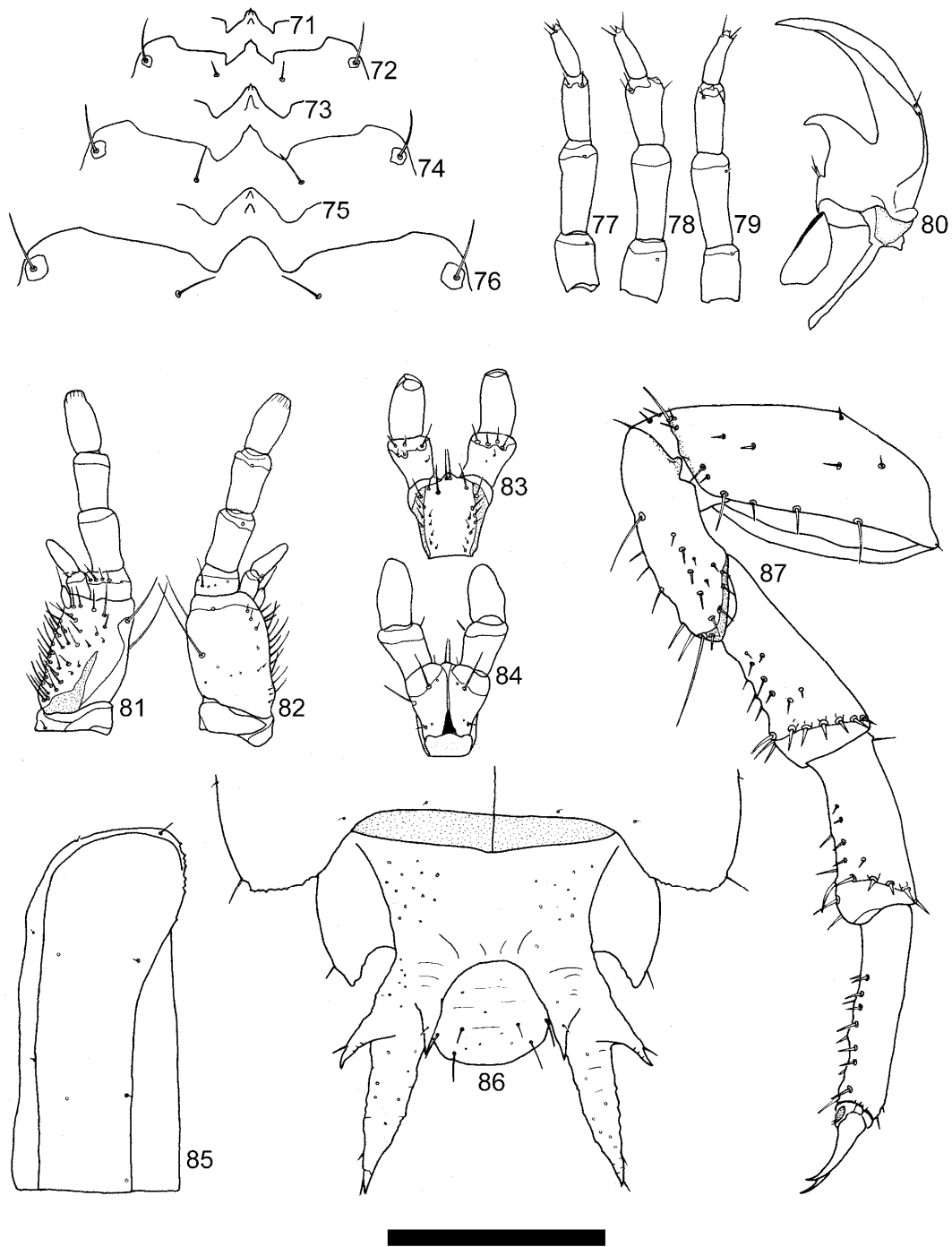
FIGURES 20-36. *Carabus asperatus* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (20); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin (21); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (22); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (23); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (24); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (25); first instar, right antenna, dorsal (26), lateral (27) and ventral aspect (28); first instar, dorsal aspect of mandible (29); first instar, right maxilla, dorsal (30) and ventral aspect (31); first instar, labium, dorsal (32) and ventral aspect (33); first instar, right urosternite V (34); first instar, urotergite IX (35); first instar, ventral aspect of left metathoracic leg (36). (Scale: 1 mm).



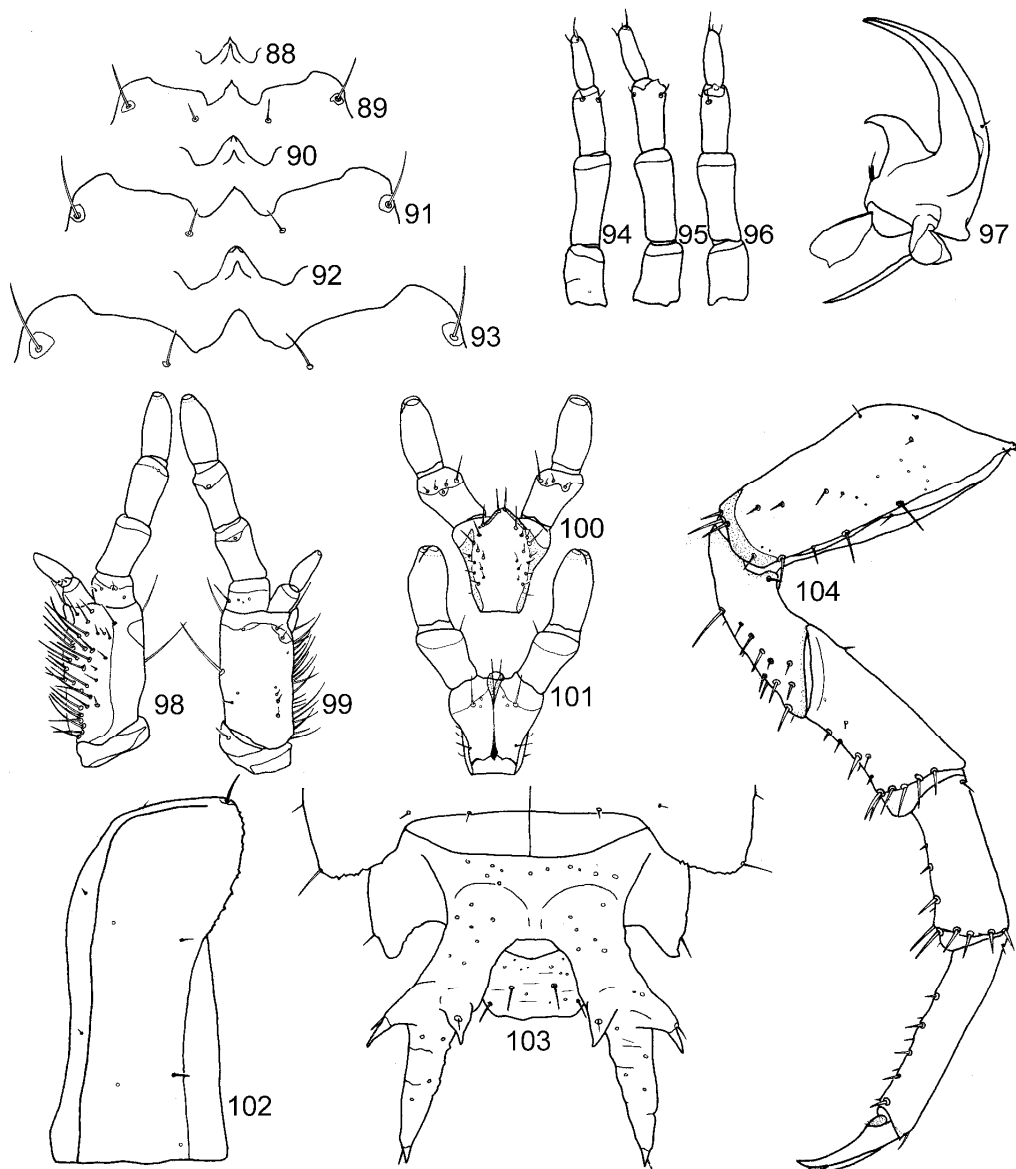
FIGURES 37-53. *Carabus stenocephalus stenocephalus* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (37); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin (38); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (39); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (40); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (41); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (42); first instar, right antenna, dorsal (43), lateral, (44) and ventral aspect (45); first instar, dorsal aspect of mandible (46); first instar, right maxilla, dorsal (47) and ventral aspect (48); first instar, labium, dorsal (49) and ventral aspect (50); first instar, right urosternite V (51); first instar, urotergite IX (52); first instar, ventral aspect of left metathoracic leg (53). (Scale: 1 mm).



FIGURES 54-70. *Carabus stenocephalus susicus* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (54); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin (55); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (56); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (57); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (58); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (59); first instar, right antenna, dorsal (60), lateral, (61) and ventral aspect (62); first instar, dorsal aspect of mandible (63); first instar, right maxilla, dorsal (64) and ventral aspect (65); first instar, labium, dorsal (66) and ventral aspect (67); first instar, right urosternite V (68); first instar, urotergite IX (69); first instar, ventral aspect of left metathoracic leg (70). (Scale: 1 mm).



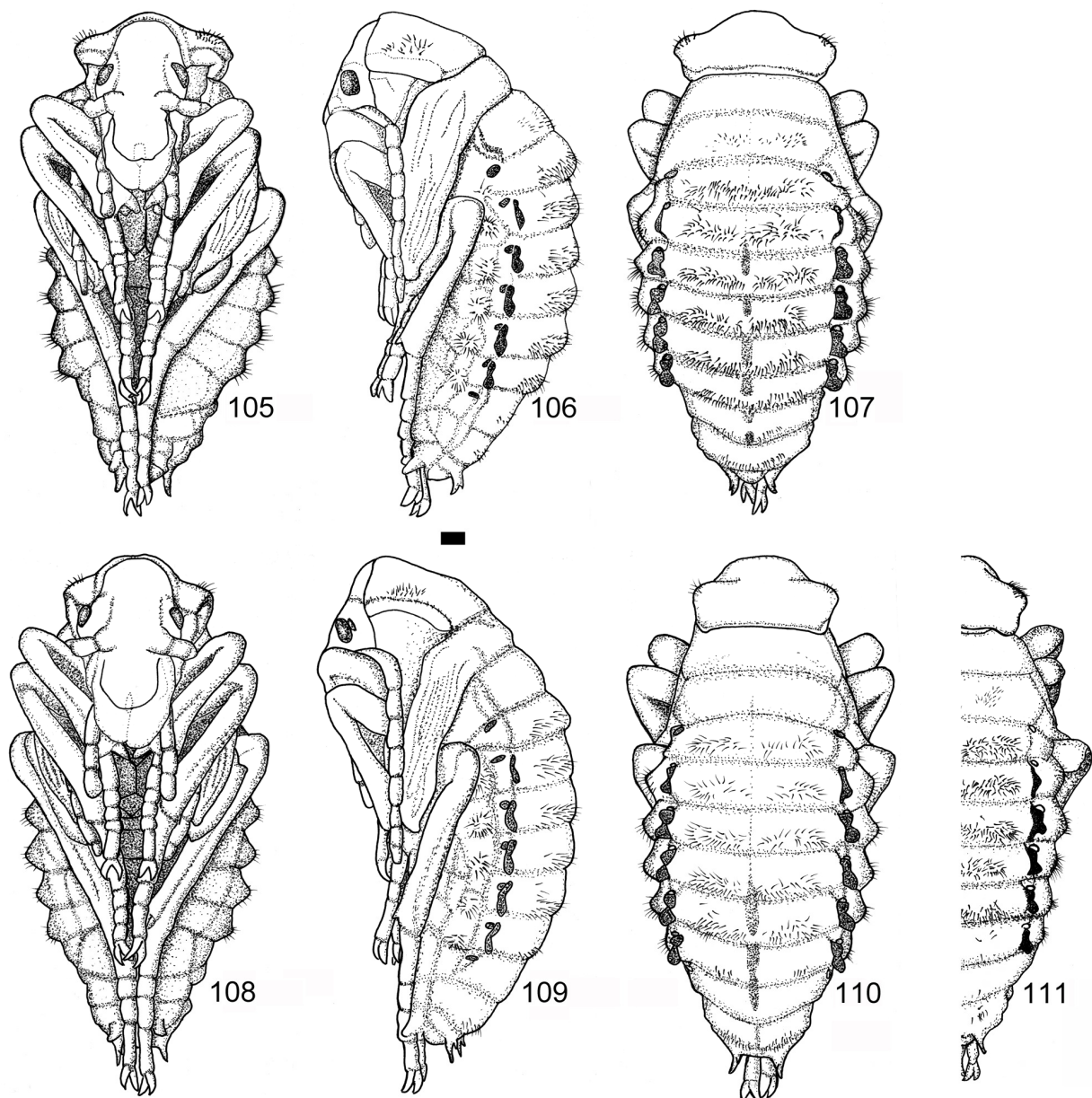
FIGURES 71-87. *Carabus stenocephalus ifniensis* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (71); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin (72); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (73); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (74); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (75); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (76); first instar, right antenna, dorsal (77), lateral, (78) and ventral aspect (79); first instar, dorsal aspect of mandible (80); first instar, right maxilla, dorsal (81) and ventral aspect (82); first instar, labium, dorsal (83) and ventral aspect (84); first instar, right urosternite V (85); first instar, urotergite IX (86); first instar, ventral aspect of left metathoracic leg (87). (Scale: 1 mm).



FIGURES 88-104. *Carabus stenocephalus aliai* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (88); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin (89); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (90); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (91); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (92); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (93); first instar, right antenna, dorsal (94), lateral, (95) and ventral aspect (96); first instar, dorsal aspect of mandible (97); first instar, right maxilla, dorsal (98) and ventral aspect (99); first instar, labium, dorsal (100) and ventral aspect (101); first instar, right urosternite V (102); first instar, urotergite IX (103); first instar, ventral aspect of left metathoracic leg (104). (Scale: 1 mm).

Pupae of *Cathoplius* show a slightly trilobate labrum and a laterally pubescent pronotum with lateral lobes present from urotergites II to IV. Urogomphi are well developed, conical, narrow and with an evident upper spina.

The pupa of *C. asperatus* (Figs. 105-107) shows tufts of setae on the metanotum (more scarce and short) and from urotergite I to VIII (more thick and long). Contrary to other taxa, in the *C. stenocephalus* pupa (Figs. 108-110) setae on metanotum are extremely thin, scarce, and barely visible and sometimes absent. Longer, thicker and stronger setae are present from urotergite I to VI and on urotergite VIII, but are absent on urotergite VII.



FIGURES 105-111. *Carabus asperatus* pupa: ventral (105), lateral (106) and dorsal aspect (107); *C. stenocephalus susicus* pupa: ventral (108), lateral (109) and dorsal aspect (110); details of *C. stenocephalus aliai* pupa, dorsal aspect (111). Habitus (Scale: 1 mm).

The pupa of *C. stenocephalus aliai* (Fig. 111) presents tufts of setae on the metanotum (thinner and barely visible, with a density similar to that present in the *C. asperatus* pupa) and from

urotergite I to V (thicker, stronger and longer), and isolated setae on urotergite VI (from 1 to 4) and VII (from 3 to 4), whereas on urotergite VIII, 10 to 15 setae, symmetrically subdivided into two small groups, are present.

Experimental crossbreeding

The results of hybridization trials between *C. asperatus* and *C. stenocephalus stenocephalus* (ASTEN 1 and 2), *C. stenocephalus ifniensis* and *C. stenocephalus susicus* (IFSU) and *C. stenocephalus ifniensis* and *C. stenocephalus aliai* (AIF 1 and 2) as well as the results of the F1 crossbreeding (ASTEN x ASTEN and AIF x AIF) are reported in Table 6.

TABLE 6. Results of the hybridization experiments: *C. asperatus* x *C. stenocephalus stenocephalus*, *C. stenocephalus ifniensis* x *C. stenocephalus susicus* and *C. stenocephalus ifniensis* x *C. stenocephalus aliai*.

Parent species (acronym of combination)	No. of breeders	Oviposition period	No. of hatched larvae / No. of emerged imagines	No. of viable imagines after 30 days from emersion (no. ♂♂, ♀♀)	Survival rate
♂ <i>C. asperatus</i> x ♀ <i>C. s. stenocephalus</i> (ASTEN1)	2♂♂ & 2♀♀	From 23/4/09 to 15/6/09	199/79	75 (45♂♂, 30♀♀)	37.7%
♂ F1 ASTEN1 x ♀ F1 ASTEN1	3♂♂ & 3♀♀	From 7/9/09 to 2/11/09	91/5	0	0
♂ <i>C. s. stenocephalus</i> x ♀ <i>C. asperatus</i> (ASTEN2)	2♂♂ & 2♀♀	From 5/4/09 to 16/6/09	221/87	80 (35♂♂, 45♀♀)	36.2%
♂ F1 ASTEN2 x ♀ F1 ASTEN2	3♂♂ & 3♀♀	From 13/9/09 to 17/11/09	127/8	0	0
♂ <i>C. s. ifniensis</i> x ♀ <i>C. s. susicus</i> (IFSU)	1♂ & 1♀	From 05/12/08 to 15/01/09	480/298	308 (190♂♂, 195♀♀)	64.2%
♂ <i>C. s. aliai</i> x ♀ <i>C. s. ifniensis</i> (AIF1)	1♂ & 2♀♀	From 30/12/10 to 12/3/11	187/72	67 (33♂♂, 34♀♀)	35.8%
♂ F1 AIF1 x ♀ F1 AIF1	2♂♂ & 2♀♀	From 8/9/11 to 3/10/11	56/0	0	0
♂ <i>C. s. ifniensis</i> x ♀ <i>C. s. aliai</i> (AIF2)	2♂♂ & 4♀♀	From 16/5/11 to 21/7/11	196/75	69 (37♂♂, 32♀♀)	35.2%
♂ F1 AIF2 x ♀ F1 AIF2	2♂♂ & 2♀♀	From 4/10/11 to 11/11/11	87/0	0	0

Morphological features of hybrids

Morphological features of the pure bred *Cathoplius* species and subspecies, as well as the ones of the hybrids obtained during this study, are shown from Fig. 112 to Fig. 131. Data reported from here forward reflect the mean aspect from the observation of 50 specimens per parent species/subspecies and per hybrid.

Cathoplius hybrids showed intermediate features when compared to parent species/subspecies. In more detail, specimens of hybrid ASTEN, IFSU and AIF were

morphologically more similar to the parent female than to the male, as occurred with hybridizations of Moroccan ground beetles belonging to Subgenus *Macrothorax* (Ghittino, personal observations).

ASTEN1 hybrid (σ *C. asperatus* x ♀ *C. stenocephalus stenocephalus*, Figs. 122-123) was more similar to *C. stenocephalus stenocephalus* (Figs. 114-115), being slightly smaller (L 26-30 mm) than hybrid ASTEN2 (σ *C. stenocephalus stenocephalus* x ♀ *C. asperatus*, Figs. 124-125) (L 27-31 mm) that was more similar to *C. asperatus* (Figs. 112-113). In general, *C. stenocephalus stenocephalus* specimens are slightly smaller than the specimens of *C. asperatus* (L 22-28 mm and 23-29 mm, respectively). The pronotum in both hybrid combinations was less transverse (PL/PW: 5.5/7.5 mm = 0.733) compared to that of *C. asperatus* (PL/PW: 5.0/8.0 mm = 0.625), with a silhouette tending to *C. stenocephalus stenocephalus* (PL/PW: 5.0/6.0 mm = 0.833). The elytral sculpture in hybrid ASTEN1 was less rough (more similar to the one of *C. stenocephalus stenocephalus*) than in hybrid ASTEN2 (more similar to that of *C. asperatus*).



FIGURES 112-121. *Carabus asperatus* imago: σ (112), ♀ (113); *C. stenocephalus stenocephalus* imago: σ (114), ♀ (115); *C. stenocephalus susicus* imago: σ (116), ♀ (117); *C. stenocephalus ifniensis* imago: σ (118), ♀ (119); *C. stenocephalus aliai* imago: σ (120), ♀ (121). Habitus.

Analogously, hybrid AIF1 (σ *C. stenocephalus aliai* x ♀ *C. stenocephalus ifniensis*, Figs. 128-129) was more similar to *C. stenocephalus ifniensis* (Figs. 118-119) being slightly larger (L 28-35 mm) than hybrid AIF2 (σ *C. stenocephalus ifniensis* x ♀ *C. stenocephalus aliai*, Figs. 130-131) (L 27-34 mm) which in turn was more similar to *C. stenocephalus aliai* (Figs. 120-121). In general, *C. stenocephalus ifniensis* specimens are larger and wider than the specimens of *C. stenocephalus aliai* (L 27-35 mm and 26-34 mm, respectively). The pronotum in both hybrid combinations was wider (PL/PW: 5.5/6.5 mm = 0.846) than that of *C. stenocephalus aliai* (PL/PW: 6/5.5 mm = 1.091) with a silhouette tending towards that seen with *C. stenocephalus ifniensis* (PL/PW: 5.5/7.0 mm = 0.786). The elytral sculpture in hybrid AIF1 was characterized by slightly marked striae with fine

punctuation (like in *C. stenocephalus ifniensis*) while in hybrid AIF2 striae were deep and punctuation was coarse (similar to *C. stenocephalus aliai*).

Also in hybrid IFSU (♂ *C. stenocephalus ifniensis* x ♀ *C. stenocephalus susicus*, Figs. 126-127) a higher morphological similarity with the parent female (*C. stenocephalus susicus*, Figs. 116-117; L 24-31 mm; PL/PW: 5.5/6.5 mm = 0.846) was evident both with respect to size, that was smaller (L 26-32 mm) than in *C. stenocephalus ifniensis* (the largest in size *Cathoplius* taxon), and elytral striae were more marked and punctuation was not as fine as in *C. stenocephalus ifniensis*.



FIGURES 122-131. ASTEN1 hybrid imago: ♂ (122), ♀ (123); ASTEN2 hybrid imago: ♂ (124), ♀ (125); IFSU hybrid imago: ♂ (126), ♀ (127); AIF1 hybrid imago: ♂ (128), ♀ (129); AIF2 hybrid imago: ♂ (130), ♀ (131). Habitus.

Discussion

Feeding behavior

In Moroccan sites where *Cathoplius* were sampled it was noticed that these ground beetles feed specifically on different snails species belonging to the Genus *Theba* Risso, 1826 (see Gittenberger & Ripken 1987; Haase et al. 2014), as reported in Table 7.

As mentioned before, in laboratory conditions only live *T. pisana* and occasionally *E. vermiculata* bought on the market were given as feed.

During the first testing in 2008, a couple of *C. asperatus* [Morocco, (Sidi Bennour) Oualidia, 45 m a.s.l., 15 March 2008, C. Ghittino & E. Busato legit] were bred applying the methodology reported by Malausa (1977) that provides beef meat and apple as feed. Despite several feeding attempts, adults did not prefer this feed and after 7-10 days they buried themselves and fell into

diapause. At the beginning of September they rose to the surface but in response to the same feed they again buried themselves after a week and died during diapause.

TABLE 7. Species of snails preyed by *Cathoplius* in Moroccan sampling sites.

TAXON	ACTUAL PREY	OTHER SNAILS PRESENT
<i>C. asperatus</i> (Dejean, 1826)	At Port Lixus (Larache): <i>Theba pisana pisana</i> (O.F. Müller, 1774) At Oualidia (Sidi Bennour): <i>Theba pisana pisana</i> (O.F. Müller, 1774) <i>Theba pisana cantinensis</i> (Sacchi, 1955) At Souira Kedima (Safi) <i>Theba pisana pisana</i> (O.F. Müller, 1774) <i>Theba subdentata helicella</i> (W. Wood, 1828)	At Port Lixus (Larache): <i>Eobania vermiculata</i> (O.F. Müller, 1774) At Oualidia (Sidi Bennour): <i>Eobania vermiculata</i> (O.F. Müller, 1774) <i>Cochlicella acuta</i> (O. F. Müller, 1774)
<i>C. stenocephalus stenocephalus</i> Lucas, 1866	At Sidi Kaouki (Essaouira): <i>Theba pisana pisana</i> (O.F. Müller, 1774) <i>Theba pisana ampullacea</i> (Pallary, 1915) <i>Theba subdentata helicella</i> (W. Wood, 1828) At Cap Rhir, Tamri (Agadir Ida-Outanane): <i>Theba pisana ampullacea</i> (Pallary, 1915) <i>Theba subdentata dehnei</i> (Rossmässler, 1846)	At Sidi Kaouki (Essaouira): <i>Helicopsis cf. welschi</i> (Pallary, 1898)
<i>C. stenocephalus susicus</i> Antoine, 1941	At Aglou Plage (Tiznit): <i>Theba pisana ampullacea</i> (Pallary, 1915) <i>Theba subdentata subdentata</i> (Férussac, 1821)	-
<i>C. stenocephalus ifniensis</i> Zarco, 1941	At Sidi Ifni (Sidi Ifni): <i>Theba subdentata meridionalis</i> (Sacchi, 1955)	-
<i>C. stenocephalus aliai</i> Escalera, 1944	At Tan-Tan (Tan-Tan): <i>Theba chudeaui</i> (Germain, 1908) <i>Theba subdentata meridionalis</i> (Sacchi, 1955)	At Tan-Tan (Tan-Tan): <i>Eremina dillwyniana</i> (Pfeiffer, 1851)

Only during subsequent experiments with other *Cathoplius* specimens sampled in November 2008 it was possible to ascertain the fact that adults of Subgenus *Cathoplius* feed exclusively on live snails and rejecting raw meat that is acceptable to other helicophagous species of the Genus *Carabus*. Furthermore, adults of *Cathoplius* as well as larvae become intoxicated if frozen snails are given as feed.

As previously reported by Prunier (1999), *Cathoplius* were not attracted by the liquid substances used for pitfall traps such as vinegar and beer. The total lack of specimens observed into pitfall traps positioned in sites where *Cathoplius* were known to be abundant (Figs. 132-133) may be explained by the fact that these attractants are both ineffective and may actually repel these ground beetles.

As exclusive predators of live *Theba* snails, *Cathoplius* play an important role in the ecosystem by reducing *Theba* proliferation which can be detrimental to both conservation of the scarce vegetation in arid areas and to animal husbandry by preventing important livestock parasitic diseases among grazing land animals. *Theba* snails are key to the life-cycle of sheep and goat lungworms acting as intermediate hosts for nematodes such as *Muellerius capillaris* (Mueller, 1889), *Cystocaulus ocreatus* (Railliet & Henry, 1907), *Protostrongylus rufescens* (Leuckart, 1865) and *Neostrongylus linearis* (Marotel, 1913). *Theba* snails harbor the infective stage (L3) of these protostrongylid worms while sheep and goats serve as the final hosts and harbor adult parasites in their lungs (Cabaret 1987; Solomon *et al.* 1999; Grewal *et al.* 2003). Sheep and goat breeding is a very common activity along the Moroccan Atlantic coast and parasitic diseases of the respiratory tract are quite widespread in these areas (Ghittino, personal observations). *Theba* snails can be vectors of dicrocoeliasis by harboring the miracidium of *Dicrocoelium dendriticum* (Rudolphi, 1819), the lancet liver fluke, a digenean trematode affecting bile ducts of cattle, sheep and sometimes man. Snails are the first intermediate host in the life cycle of the parasite while ants are

the second intermediate host with the final hosts being mainly sheep, rarely goats and camels. The final hosts get infected by eating grass contaminated with ants harboring *D. dendriticum* metacercariae (Mas-Coma & Bargues 1997). In Morocco, chemical control of snails with pesticides is widely practiced, which also is aimed at prevention of human schistosomiasis that is endemic in some areas (Belkacem & Jana 2006). Chemical control can be harmful for the environment and ingestion of molluscicides such as metaldehyde or methiocarb can be toxic for domestic and wild animals. In contrast, biological control is an environmentally sound and effective means for reducing or mitigating pests and pest effects. By using natural enemies such as helicophagous ground beetles, a control of *Theba* populations could be achieved. Conservation of *Cathoplius* on the Moroccan Atlantic coast is therefore essential.



FIGURES 132-133. Typical *Carabus asperatus* biotope: dune area at the outlet of Oued Tensift, Souira Kedima, commune rurale de Lamaachate, province de Safi, Morocco (132); typical *Carabus stenocephalus* biotope: dune area around Tamri, province de Agadir Ida-Outanane, Morocco (133).

Life-cycle

The *Cathoplius* life-cycle belongs to the winter breeding type *sensu* Paarman (1979) and partially to the annual univoltine winter iteroparous type *sensu* Matalin (2007) both of which are typical of ground beetles species living in areas where winter temperatures exceed 5°C. This type of reproduction occurs from late autumn to early spring, and larval development is completed during the cold season, with adults of the new generation emerging in late winter and in spring and undergoing a dormancy in summer or a summer parapause. In the case of *Cathoplius* species and subspecies, beginning of reproduction depends on the start of the raining season (Paarmann 1979) which normally occurs in autumn (Northern Morocco) or in winter (Southern Morocco).

In our breeding trials, we noticed that only *C. stenocephalus aliai* belongs exactly to the reproduction type *sensu* Matalin (2007) where adults of the parental generation die after the breeding period ends. We observed adults of the new generation emerging in late winter-early spring, undergoing a diapause from spring to autumn, rising to the surface in late autumn-winter, then breeding during winter and dying just after reproduction.

In *C. asperatus* and all the other *C. stenocephalus* subspecies adults who bred in late autumn-early winter, after a short diapause, become active again and breed a second time in late winter-early spring. Moreover, in these taxa adults of the first generation, after sclerification and a short burial period, start breeding immediately. In this way, in spring an overlapping of two different generations of larvae occurs, those produced by old breeders and those by new breeders. Then, old and new breeders, as well as adults newly generated from both of them, undergo summer diapause. For these reasons it was impossible to precisely place the life-cycle of *C. asperatus* and three of four subspecies of *C. stenocephalus* (*C. stenocephalus stenocephalus*, *C. stenocephalus susicus*, *C. stenocephalus ifniensis*) into one of the typologies proposed by Matalin (2007).

Under laboratory conditions *Cathoplius* can have an average life span of 1-1.5 years (with the exception of *C. stenocephalus aliai*) during which they can reproduce up to three times, although progressively less effectively with each subsequent attempt. Worthy of notice is that by creating ideal environmental conditions a partial summer breeding can also be obtained although this does not occur in the natural environment.

While we cannot explain the shortened life cycle of *C. stenocephalus susicus* under laboratory conditions, the shorter cycle of *C. stenocephalus aliai* is likely due to the desert habitat. In this habitat, the period of activity of snails is reduced to periods when the rain falls. In contrast, the duration of the pupal instar can be extended into the cell until following rainy season without causing any damage to the pupa.

Fecundity and reproductive strategies

One of the most striking features observed during our breeding experiments was the high fecundity rate of *Cathoplius*. Species belonging to this Subgenus of *Carabus* were found to be one of the most prolific among the known ground beetles. Thiele (1977) reported high fecundity in ground beetles under laboratory conditions. He found that a single female of *Calosoma sycophanta* Linnaeus, 1758, laid up to 653 eggs over a period of 2-3 years. *Pterostichus chalcites* Say, 1823, in a single breeding season laid up to 351 eggs per female. Generally, in the Genus *Carabus*, reproductive rates are much lower even though high numbers of laid eggs per specimen (up to 200-300 in two-three years) are reported (Sturani 1962; Casale *et al.* 1982).

In our experiments, *Cathoplius* females laid from a minimum of 241 eggs (*C. asperatus*) to a maximum of 511 eggs (*C. stenocephalus susicus*) per reproduction cycle, in a period of time varying from 50 to 100 days and with an oviposition rate of 4-12 eggs per day. Prunier (1999), in

his breeding experiments, reported that females of *C. stenocephalus stenocephalus* laid a total of 30-40 eggs in a week with an oviposition rate of 5 eggs per day. These lower fecundity rates may be due to the females he used, which when collected were likely at the end of their reproduction cycle.

The reproductive strategy adopted by the species of Subgenus *Cathoplius* is clearly of “r” type (MacArthur & Wilson 1967) and is based on their reproduction potential. The general theory of the “r” or “K” type reproductive strategies is often criticized (Reznick *et al.* 2002) but in the species of ground beetles dwelling in unstable habitats (such as arid areas) or habitats where prey are scarce or with a short phenology, it is common to observe high reproductive rates and/or very short life-cycles.

Cathoplius populations show a remarkable capacity of “invasion” in the environment. In a short time a contemporaneous hatching of hundreds of individuals takes place when environmental conditions are favorable (e.g. heavy rains in xeric or subdesert/desert areas that are ending in a few days). Population increases and rapid colonization of the environment reaches a peak depending on temperature and humidity conditions and on the availability of snails. Alternate phases may be characterized by population levels that approach non sustainability and result in sudden decreases. In species with “r” type strategy individuals develop rapidly and reach maturity in a short period of time. Despite high mortality rates, the high fecundity and frequent generation replacement can guarantee intensive growth rates and the preservation of the population.

Larval feeding and defense attitude

As already observed by Sturani (1962) and one of the authors (E. B.) in other *Carabus* species, when attacking a snail *Cathoplius* larvae penetrate inside the shell by keeping their ventral side of the body adhering to the shell walls, with no contact with the mollusk body. This avoids filling of their respiratory stigmata with mucus.

In *Cathoplius* larvae, an extreme specialization to the helicophagous predatory behavior is evident. In field, we were able to find larvae inside snails either on the ground or on vegetation. Being very agile, the larvae were able to reach prey by climbing on bushes (in Southern Morocco, particularly on bushes of *Launaea arborescens*). The curious behavior adopted by *Cathoplius* larvae to induce eversion of snails was never observed before in any other helicophagous ground beetle. This predation strategy seems to be very successful to prevent suffocation.

The fear response adopted by *Cathoplius* larvae when disturbed is identical to that reported for *Carabus (Macrothorax) planatus* Chaudoir, 1843 (Busato & Casale 2005). The defense attitude shown when larvae are touched on the back is common to the majority of *Carabus* species (Busato, personal observations).

Larval morphology

C. asperatus and *C. stenocephalus stenocephalus* larvae were synthetically described by Arndt *et al.* (1994), while those of *C. stenocephalus susicus*, *C. stenocephalus ifniensis* and *C. stenocephalus aliai* are here described for the first time. Arndt *et al.* (1994) reported that no macroscopic features were capable of discriminating *C. asperatus* from *C. stenocephalus* larvae. In our studies, we noticed the following differences:

- The general aspect reflects that of adults. *C. asperatus* larvae are more stocky than those of *C. stenocephalus*, a feature that is more evident when *C. asperatus* larvae are compared to those of the most geographically distant *C. stenocephalus* subspecies. *C. stenocephalus aliai* larvae are the most slender within the Subgenus.

- Size (Table 2): *C. asperatus* larvae (Fig. 15) are as large as those of *C. stenocephalus stenocephalus* (Fig. 16) and *C. stenocephalus aliai* (Fig. 19) but they are shorter than the larvae of the remaining *C. stenocephalus* subspecies (Figs. 17-18).
- Appendages: in *C. asperatus*, antennae, mouth parts and legs are markedly shorter than in *C. stenocephalus* (in the broad sense), even though length ratios between segments are the same.
- Length/width (l/w) ratio of *frontoclypeolabrum* (Table 4): this ratio follows an opposite trend in the two taxa. In *C. asperatus* the *frontoclypeolabrum* of the first instar is slightly wider than long, it is less wider in the second instar and it gets longer than wide in the third instar, while in *C. stenocephalus* the *frontoclypeolabrum* of the first instar is barely longer than wide and it gets progressively wider than long in subsequent instars.

The chaetotaxy of all taxa is identical. Sporadically and individually, some of the described setae can be present or absent.

Pupal morphology

Pupal features of Subgenus *Cathoplius*, described here for the first time, are similar to those known for the species of Subgenus *Macrothorax* Desmarest, 1850 (Busato & Casale 2005). Pupal chaetotaxy was found to be the only diagnostic character capable of discriminating the various taxa of Subgenus *Cathoplius*.

Generally, the thin setae of the metanotum, which are always present in *C. asperatus*, are frequently absent or reduced in number or present in scarce clusters in *C. stenocephalus* (in the broad sense). An exception is *C. stenocephalus aliai*, where the tufts of setae on metanotum have the same thickness of those present in the *C. asperatus* pupa even though they are thinner and barely visible. In *C. asperatus*, thick tufts of longer and stronger setae are visible from urotergite I to VIII. In *C. stenocephalus* (in the broad sense), the same setae are present from urotergite I to VI and on urotergite VIII while they are absent on urotergite VII. An exception is *C. stenocephalus aliai* where setae on urotergite VI are almost absent.

These data confirm the specific differentiation between *C. asperatus* and *C. stenocephalus* (in the broad sense).

Pre-imaginal morphology and phylogeny

Larval characters clearly place Subgenus *Cathoplius* into the phyletic lineage of Neocarabi (Arndt *et al.* 1994), confirming it as a monophyletic and homogeneous assemblage within the Genus *Carabus*, due to the numerous larval synapomorphies (more or less arched or pyramidal nasal, adnasal with a “S” shape, reduced adnasal setae).

The monophyly of Neocarabi is well supported, based on both imaginal, larval and molecular characters. The group was recognized but named differently by several authors: «Neocarabus» (Bengtsson 1927), «Rostrilabres» (Lapouge 1930), «*Longimandibulares*» (Breuning 1932–1937), and «Procrustimorphi» (Imura 1996) (Deuve *et al.* 2012). Recently, several taxa (Arcifera, *Ctenocarabus* and *Cathoplius*) were excluded from this subdivision (Deuve 2004). As already shown by other molecular studies, the Neocarabi *sensu* Deuve are recovered as monophyletic and could also include their sister-lineage *Cathoplius* (Deuve *et al.* 2012). The relationships among these clades differ between nuDNA and mtDNA topologies and are always weakly supported.

Certain larval characters indicate an early cladogenesis of *Cathoplius* compared to that of the remainder of the Neocarabi. These include the peculiar combination of both plesiomorphic and apomorphic characters in chaetotaxy, involving the presence of the ME₁, ME₈, ME₉, TE₇, TE₁₁ setae

and the lack of setae on the second antennal segment in *Cathoplius* (Arndt *et al.* 1994). This is in agreement with Deuve *et al.* (2012) who claim that in the all DNA topology, as well as in the nuDNA analyses, Cathopliogenici should be recovered as a sister group to Neocarabi with moderate support. Unfortunately, molecular analyses to date do not provide a molecular clock capable of dating the separation between *Cathoplius* and the remaining contingent of Neocarabi (Andújar *et al.* 2012 b; Deuve *et al.* 2012). The limited and peculiar distribution of the Subgenus *Cathoplius* in an area where the greater diversification of Subgenus *Macrothorax* has occurred, as well as the larval features previously reported, should confirm the phylogenetic relationship between these two subgenera.

Some of the biological data stressed in our studies can be useful to reconstruct the phylogeny of *Cathoplius* and its closely related groups. For example, in *Cathoplius* some characteristics peculiar to Carabi *brevimandibulares* (*sensu* Breuning), like egg size and oviposition modality, are present. These include eggs that are smaller and narrower compared with those of Carabi *longimandibulares* (in the wider sense), and females that dig an oblique gallery where they lay several eggs at a more or less regular distance. On the contrary, in Carabi *longimandibulares* (*sensu* Breuning) the females dig a vertical small well at the end of which a single cell for each single egg is built (Sturani 1962). In our trials it was impossible to establish the total number of laid eggs in each single gallery but this was likely corresponding to the daily oviposition rate reported in Table 1. Furthermore, the oviposition depth was probably dependent on the moisture of the surface soil.

The above cited behavior of Carabi *brevimandibulares*, known for *C. (Archicarabus) monticola* Dejean, 1826 and *C. (A.) nemoralis* O.F. Müller, 1764 (Archicarabomorphi), but also for *C. (Tachypus) cancellatus* Illiger, 1798 (Tachypogenici), was reported by Sturani (1962) and Casale *et al.* (1982). Even considering the limits that this behavior could indicate (ecological convergence in phylogenetically distant taxa), we have to remark the fact that the representatives of Archicarabomorphi and Tachypogenici, differently from *Cathoplius*, are neither sabulicolous nor steppe or desert dwellers, are not helicophagous, and have no morphological features modified in that sense. This seems to confirm that the *brevimandibulares* and *longimandibulares* lineages of *Carabus* proposed in ancient taxonomic treatments are mere polyphyletic assemblages.

Experimental crossbreeding

In *C. asperatus* x *C. stenocephalus stenocephalus* crossbreeding (ASTEN), both hybridizations (ASTEN1 and ASTEN2) caused a reduction in progeny compared to that observed in the respective parental taxa: a reduced hatching ratio (104 larvae per female in average for hybrids ASTEN, compared to 241 in *C. asperatus* and 288 in *C. stenocephalus stenocephalus*) and a low reproduction success (mean survival rate of 36.9% in hybrids ASTEN, compared to 72% in *C. asperatus* and 60% in *C. stenocephalus stenocephalus*) was noticed in all our experiments. Additionally, specimens of the F1 when crossed with one another (ASTEN x ASTEN) showed reduced fertility (36 larvae in average per female), neonatal mortality (scarcely viable pre-imaginal stages) and stillbirth (100% non viable images). Results of hybridization are therefore indicative of a remarkable genetic distance between *C. asperatus* and *C. stenocephalus stenocephalus* and corroborate the distinction at a species level of the two taxa.

In *C. stenocephalus ifniensis* x *C. stenocephalus aliai* crossbreeding (AIF), both hybridizations (AIF1 and AIF2) were also responsible for a reduction in progeny: a reduced hatching ratio (71 larvae per female in average for hybrids AIF, compared to 237 in *C. stenocephalus aliai* and 242 in *C. stenocephalus ifniensis*) and a low reproduction success (mean survival rate of 35.5% in hybrids AIF, compared to 51% in *C. stenocephalus aliai* and 50.2% in *C. stenocephalus ifniensis*) was evident. As in the hybridizations of *C. asperatus* and *C. stenocephalus*

stenocephalus, specimens of the F1 when crossed with one another (AIF x AIF) showed reduced fertility (35 larvae in average per female), neonatal mortality (scarcely viable pre-imaginal stages) and stillbirth (100% non viable images). Again, this reproductive failure is indicative of a certain genetic distance between *C. stenocephalus ifniensis* and *C. stenocephalus aliai* and could be an index of specific differentiation of the two taxa.

Contrary to what was observed in the previous hybridizations, the crossbreeding between a *C. stenocephalus ifniensis* male and a *C. stenocephalus susicus* female (IFSU) did not cause any progeny reduction: hatching ratio (480 larvae per female) was comparable to the one of *C. stenocephalus susicus* (467 larvae in average). Reproduction success and the great viability of the F1 (mean survival rate of 64.2%) confirmed the close relationship of the two taxa and their attribution to the same species; for this reason, the attempt of crossing with one another the F1 specimens of hybrid IFSU was not carried out.

General conclusions and biogeographic remarks

Subgenus *Cathoplius*, within the Genus *Carabus* (in the broad sense), form a very homogenous and peculiar lineage of strictly helicophagous ground beetles adapted to arid, steppe or sub-desert areas, localized along the Moroccan Atlantic coast. Both pre-imaginal features and life-cycle as described and illustrated in this paper confirm its taxonomical position in an isolated section Cathopliogenici. Nevertheless, in *Cathoplius* some characteristics peculiar to Carabi *brevimandibulares* (*sensu* Breuning), like the small egg size and oviposition modality, are present.

The *Cathoplius* life-cycle belongs to the winter breeding type and occurs from late autumn to early spring. The most striking result of our breeding trials was the high fecundity rate of *Cathoplius*. Taxa belonging to this subgenus were found to be one of the most prolific among the known ground beetles, showing a remarkable capacity of invasion in the environment in a short period of time when environmental conditions are favorable and snails are available.

The results of our hybridization trials indicate a remarkable genetic distance between *C. asperatus* and *C. stenocephalus* (in the broad sense), and corroborate the distinction at a species level of the two taxa. Furthermore, they indicate a marked genetic distance between *C. stenocephalus ifniensis* and *C. stenocephalus aliai*, which could suggest that the latter is a distinct species.

Finally, it is important to discuss the high biogeographical interest in the Subgenus *Cathoplius* and its enigmatic origin, evolutionary story and present geographical distribution. Through molecular analyses, Cathopliogenici are a recovered sister to Neocarabi with moderate support (Deuve *et al.* 2012) and this result is consistent with their similar larval morphology (Arndt *et al.*, 1994). Currently, Neocarabi include an assemblage of many subgenera of *Carabus* widely spread throughout the Palaearctic and Nearctic regions, subdivided into three main clades (Kim *et al.* 2008; Deuve *et al.* 2012). One of them, the “MIC clade” (Deuve 2008), comprises Subgenera *Macrothorax*, *Iniopachus* and *Chrysocarabus*, and includes all derived helicophagous species. Despite the singular morphological features of *Cathoplius* adults, in this contribution we demonstrated that both larval and pupal characters suggest a close relationship of *Cathoplius* with *Macrothorax*. The latter is a Western Mediterranean lineage, represented also in North Africa, whereas the extant *Iniopachus* and *Chrysocarabus* species are limited to Europe. In contrast, no *Cathoplius* species are represented in Europe, nor in the Mediterranean area or Macaronesian islands. The subgenus is today peculiarly localized in a narrow fringe along the Atlantic coast of Northwestern Africa, approximately 1200 kilometers in length (Fig. 134).

This fact has greatly limited any hypothesis on the origin and evolution of the Cathopliogenici lineage. An extensive literature, based on molecular data and paleogeographic

maps, is now available on the separation of pairs of Betic-Riffian taxa with the opening of the Gibraltar Strait at the end of the Messinian (5.3 Mya) (Prüser & Mossakowski 1998; Andújar *et al.* 2012 b), the split between the Moroccan *C. (Mesocarabus) riffensis* and the Iberian *Mesocarabus* (Andújar *et al.* 2012 a), and the single event of colonization of the Canary islands by the common ancestor of *Nesaeocarabus* and *Eurycarabus* from the Western coast of Africa from 10 to 7 Mya (Colas 1961; Prüser *et al.* 2000; Penev *et al.* 2003). However, there is still uncertainty on the calibration of the molecular clock and the estimation of cladogenetic ages in the Genus *Carabus* (Andújar *et al.* 2012 b, Deuve *et al.* 2012).

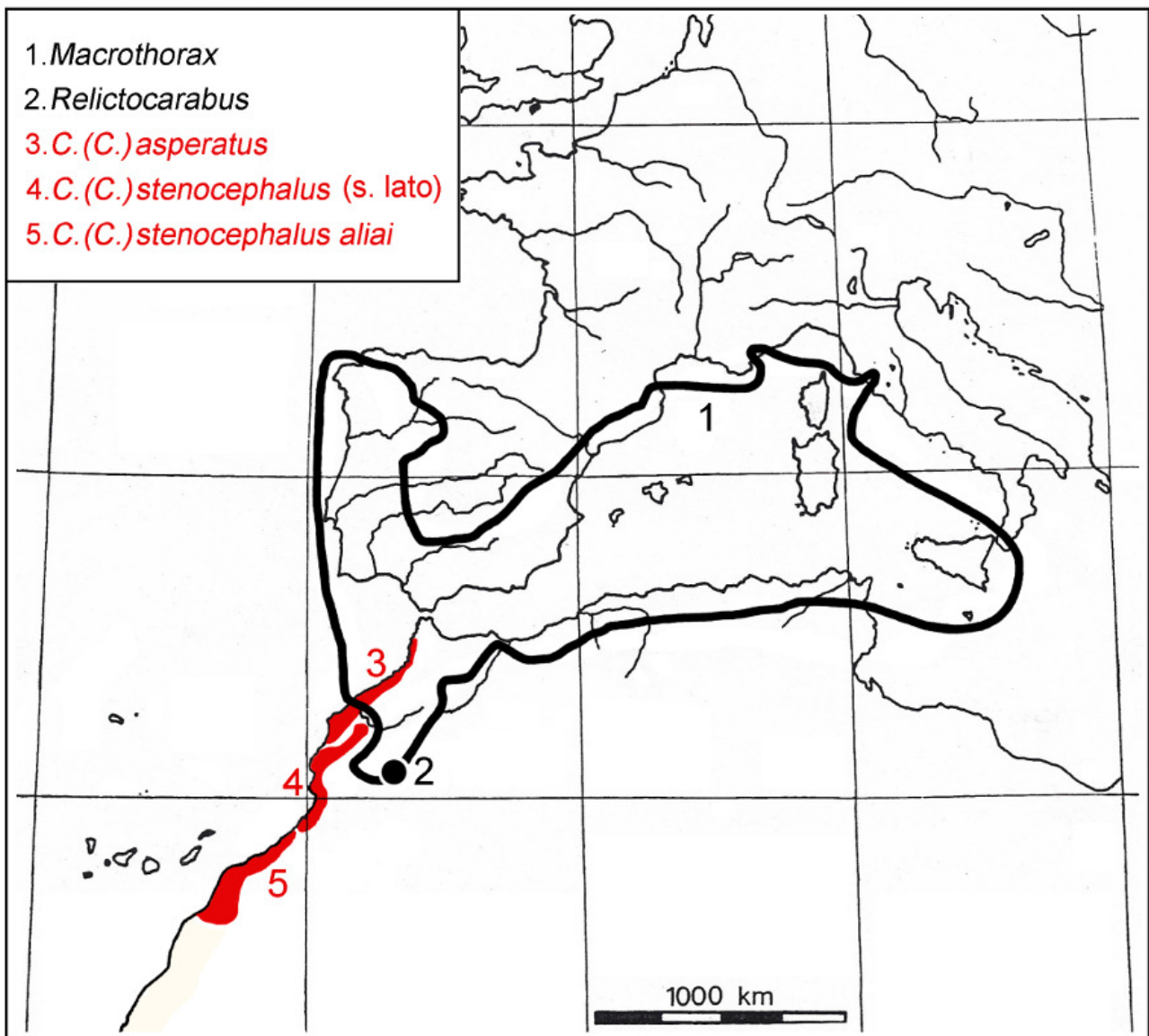


FIGURE 134. Distribution map of *Carabus* of Subgenus *Cathoplius*, together with related Subgenus *Macrothorax* (four species) and *Relictocarabus meurguesianus*.

To date there are no hypotheses for the origin and age of *Cathopliogenici*, or dating of the separation between *Cathoplius* and the remaining contingent of *Neocarabi*. *Cathoplius* is the only extant *Carabus* lineage endemic to the African continent. The limited and peculiar distribution of this subgenus in an area where the greater diversification of Subgenus *Macrothorax* has occurred, as well as the pre-imaginal features previously reported, strongly suggests the phylogenetic relationship between these two subgenera. Currently, we can propose that *Cathopliogenici*, early

isolated from the Iberian stock of the *Macrothorax* lineage on the High Atlas in Late Middle Miocene (12-11 Mya) (Popov *et al.* 2004), later radiated in the Mid-Vallesian Crisis (9.6 Mya), which induced the development of open habitats and extinction of faunas associated with forests (Eronen *et al.* 2009; Deuve *et al.* 2012). These dramatic environmental and climatic changes may have resulted in a split from a common ancestor of *C. (Macrothorax) morbillosus* that was able to survive at high altitude on the High Atlas [now represented by *C. (Relictocarabus) meurguesianus* Ledoux, 1984]. In contrast, at low altitude, along the wet Atlantic coast, *Cathoplius* developed peculiar features, strategies and way of life adapted to sandy and steppe habitats. *Cathoplius* and *Macrothorax* are nowadays widely geographic substitutes (Fig. 134).

An equally interesting question centers with the paleogeographic and paleoclimatic events that could have split the two currently recognized species of *Cathoplius*, i.e. *asperatus* and *stenocephalus*, along the very homogeneous, uniform fringe of the Western coast of Morocco. *C. (C.) asperatus* and *C. (C.) stenocephalus* are today substitutive species in the area around the outlet of Oued Tensift (South of Safi), while *C. stenocephalus escalerae* was able to colonize inner steppe zones in the area of Ben Guerir (North of Marrakech) (J. Kaláb legit). Oued Tensift, which rises from the western slopes of the High Atlas, does not presently or in the recent past represent a significant geographical barrier for dispersal of brachypterous ground beetles. Therefore, we believe that speciation and subspeciation events within *Cathoplius* require additional explanations. These might include vicariance (i.e. development of geographic and/or environmental barriers) and dispersal power (presumably low in these specialized carabids) that have to be associated with a reliable molecular clock calibrated to the paleogeographic and paleoclimatic evolution of the High Atlas and the Northern Saharan areas. While not the central theme of the current report, we can merely hypothesize that the early cladogenetic events splitting *asperatus* from *stenocephalus* occurred North and South of the High Atlas chain since the Upper Miocene to Middle Pliocene in connection with the increased aridity of these areas. Later, Pleistocene climatic changes, with alternate extensions of savanna, steppe and desert biomes, could explain the differentiation and isolation of the subspecies of *C. stenocephalus*, and the localization of *C. stenocephalus aliai* in the Saharan area of Southwestern Morocco. Future and more in-depth investigations are needed to determine the conditions responsible for the evolution and current distribution of this unique, peculiar and fascinating lineage of *Carabus*.

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Captions of figures

FIGURES 1-4. *Carabus stenocephalus susicus* adult preying a small *Eobania vermiculata* (1); mating adults of *C. stenocephalus aliai* (2); *C. stenocephalus ifniensis* female while laying (3); *C. asperatus* eggs laid on moss (4).

FIGURES 5-10. *Carabus stenocephalus susicus* 3rd instar larva that underwent ecdysis into a cell dug under a surface shelter (5); *C. stenocephalus susicus* 3rd instar larva after ecdysis into a cell dug deep in the soil (visible in transparency through the breeding container) (6); *C. stenocephalus susicus* 3rd instar larva that underwent ecdysis into a *Theba* snail: exuviae were pushed externally (7); exuviae of a *C. stenocephalus stenocephalus* 2nd instar larva into a preyed snail (8); *C. asperatus* pupa into a cell dug at a depth of 6.5 cm (9); *C. asperatus* pupa into a cell dug under a surface shelter (10).

FIGURES 11-14. Partly pigmented pupa of *Carabus asperatus* close to emergence (11); Pigmentation phases in a neo-emerged *Carabus stenocephalus stenocephalus* male: right after emergence (12); after two hours from emergence (13); at almost complete pigmentation (14).

FIGURES 15-17. Dorsal aspect of the first instar larva of: *Carabus asperatus* (15); *C. stenocephalus stenocephalus* (16); *C. stenocephalus susicus* (17). Habitus (Scale: 1 mm).

FIGURES 18-19. Dorsal aspect of the first instar larva of: *Carabus stenocephalus ifniensis* (18); *C. stenocephalus aliai* (19). Habitus (Scale: 1 mm).

FIGURES 20-36. *Carabus asperatus* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (20); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin

(21); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (22); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (23); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (24); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (25); first instar, right antenna, dorsal (26), lateral (27) and ventral aspect (28); first instar, dorsal aspect of mandible (29); first instar, right maxilla, dorsal (30) and ventral aspect (31); first instar, *labium*, dorsal (32) and ventral aspect (33); first instar, right urosternite V (34); first instar, urotergite IX (35); first instar, ventral aspect of left metathoracic leg (36). (Scale: 1 mm).

FIGURES 37-53. *Carabus stenocephalus stenocephalus* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (37); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin (38); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (39); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (40); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (41); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (42); first instar, right antenna, dorsal (43), lateral, (44) and ventral aspect (45); first instar, dorsal aspect of mandible (46); first instar, right maxilla, dorsal (47) and ventral aspect (48); first instar, *labium*, dorsal (49) and ventral aspect (50); first instar, right urosternite V (51); first instar, urotergite IX (52); first instar, ventral aspect of left metathoracic leg (53). (Scale: 1 mm).

FIGURES 54-70. *Carabus stenocephalus susicus* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (54); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin (55); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (56); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (57); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (58); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (59); first instar, right antenna, dorsal (60), lateral, (61) and ventral aspect (62); first instar, dorsal aspect of mandible (63); first instar, right maxilla, dorsal (64) and ventral aspect (65); first instar, *labium*, dorsal (66) and ventral aspect (67); first instar, right urosternite V (68); first instar, urotergite IX (69); first instar, ventral aspect of left metathoracic leg (70). (Scale: 1 mm).

FIGURES 71-87. *Carabus stenocephalus ifniensis* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (71); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin (72); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (73); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (74); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (75); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (76); first instar, right antenna, dorsal (77), lateral, (78) and ventral aspect (79); first instar, dorsal aspect of mandible (80); first instar, right maxilla, dorsal (81) and ventral aspect (82); first instar, *labium*, dorsal (83) and ventral aspect (84); first instar, right urosternite V (85); first instar, urotergite IX (86); first instar, ventral aspect of left metathoracic leg (87). (Scale: 1 mm).

FIGURES 88-104. *Carabus stenocephalus aliai* larva: first instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (88); first instar, dorsal aspect, *frontoclypeolabrum* anterior margin (89); second instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (90); second instar, dorsal aspect, *frontoclypeolabrum* anterior profile (91); third instar, ventral aspect, details of the *frontoclypeolabrum* central lobe (92); third instar, dorsal aspect, *frontoclypeolabrum* anterior profile (93); first instar, right antenna, dorsal (94), lateral, (95) and ventral aspect (96); first instar, dorsal aspect of mandible (97); first instar, right maxilla, dorsal (98) and ventral aspect (99); first instar, *labium*, dorsal (100) and ventral aspect (101); first instar, right urosternite V (102); first instar, urotergite IX (103); first instar, ventral aspect of left metathoracic leg (104). (Scale: 1 mm).

FIGURES 105-111. *Carabus asperatus* pupa: ventral (105), lateral (106) and dorsal aspect (107); *C. stenocephalus susicus* pupa: ventral (108), lateral (109) and dorsal aspect (110); details of *C. stenocephalus aliai* pupa, dorsal aspect (111). Habitus (Scale: 1 mm).

FIGURES 112-121. *Carabus asperatus* imago: ♂ (112), ♀ (113); *C. stenocephalus stenocephalus* imago: ♂ (114), ♀ (115); *C. stenocephalus susicus* imago: ♂ (116), ♀ (117); *C. stenocephalus ifniensis* imago: ♂ (118), ♀ (119); *C. stenocephalus aliai* imago: ♂ (120), ♀ (121). Habitus.

FIGURES 122-131. ASTEN1 hybrid imago: ♂ (122), ♀ (123); ASTEN2 hybrid imago: ♂ (124), ♀ (125); IFSU hybrid imago: ♂ (126), ♀ (127); AIF1 hybrid imago: ♂ (128), ♀ (129); AIF2 hybrid imago: ♂ (130), ♀ (131). Habitus.

FIGURES 132-133. Typical *Carabus asperatus* biotope: dune area at the outlet of Oued Tensift, Souira Kedima, commune rurale de Lamaachate, province de Safi, Morocco (132); typical *Carabus stenocephalus* biotope: dune area around Tamri, province de Agadir Ida-Outanane, Morocco (133).

FIGURE 134. Distribution map of ground beetles of the Cathopliogenici lineage, together with related Neocarabi of Subgenus *Macrothorax* (four species) and *Relictocarabus meurguesianus*.