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Larvae of the supertribe Siagonitae: genera *Siagona* LATREILLE and *Enceladus* BONELLI (Coleoptera: Carabidae)

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Abstract

Larvae of *Siagona* sp. and *Enceladus gigas* BONELLI are described and illustrated and a preliminary larval diagnosis of the supertribe Siagonitae is proposed. The monophyly of the supertribe is supported by several synapomorphic larval character states. The studied larvae of Siagonitae share no significant apomorphies with those of other carabids and the phylogenetic position of the supertribe remains uncertain.

Key words: Coleoptera, Adephaga, Carabidae, Siagonitae, *Siagona*, *Enceladus*, larvae, description, morphology, phylogeny, Africa, Mali, South America, Trinidad, Brazil.

Introduction

The supertribe Siagonitae is predominantly a tropical group of carabid beetles consisting of two tribes and four genera. The tribe Siagonini includes *Siagona* LATREILLE, 1804 with about 60 species in the Oriental and Afrotropical Regions with some species in the Mediterranean, *Siagonella* LECORDIER, 1977 with four species in Africa and *Luperca* LAPORTE, 1840 with one species in India and another in tropical Africa. The second tribe Enceladini includes the monobasic *Enceladus* BONELLI, 1813 from the northern part of South America. Immature stages have been described for two species of the supertribe: *Siagona* cf. *brunnipes* DEJEAN, 1825 by MOORE (1972) and *Enceladus gigas* BONELLI, 1813 by ERWIN (1978).

The purpose of the present paper is to redescribe larvae of the genera *Siagona* and *Enceladus* based on the study of additional specimens and illustrate their morphology. In addition, the preliminary larval description and diagnosis of the supertribe is proposed and the phylogeny of Siagonitae based on larval character states is discussed.

Material and methods

This work is based on a study of three slide-mounted larvae: two of *Enceladus gigas* (collected in Trinidad, "Caparo", 2.III.1910 and in Brazil, Roraima, Ireng River, 12.VII.1911) and one larva of *Siagona* sp. (collected in Africa, Mali, Dari, 14°22'N; 04°45'W, XI.1965, in pitfall trap, leg. R. Farrow). Three more larvae of *Enceladus gigas* from Trinidad, "Caparo" collected in 1910 and 1911 were available in alcohol and briefly compared under low magnification. All larvae were field-collected. Collectors of *Enceladus* larvae are unknown. Larvae of *Siagona* sp. and *Enceladus gigas* were borrowed for study from the Natural History Museum, London. U.K. (NHML) and National Museum of Natural History, Washington, D.C., U.S.A. (NMNH) respectively.

Larvae were mounted on microscope slides in Hoyers (*Siagona*) or Euparal (*Enceladus*) mediums and studied with a Wild microscope at magnification up to 50 X or with a compound microscope

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MBI-1 at magnifications up to 400 X. Morphological drawings were prepared using a Wild or Reichert camera lucida for these microscopes respectively. All measurements were made using a micrometre. Terms of larval morphology follow LAWRENCE (1991). Notation of primary setae and pores follows BOUSQUET & GOULET (1984). Homologization of many sensilla is hardly possible due to numerous modifications of the studied larvae. In many cases I was uncertain about precise homology of sensilla on cephalic capsule; however, I prefer to designate them tentatively to be able to refer on the sensilla in the description.

Larvae of both taxa studied share a significant number of character states which are combined below under the description of the supertribe and are not repeated for each genus. It should be mentioned, however, that the proposed diagnosis and description of the supertribe are tentative and will be modified when additional material is available.

Supertribe Siagonitae

DIAGNOSIS. Larvae of the supertribe Siagonitae may be readily recognized within those of the family Carabidae by having seta MN1 on lateral side of mandible absent and seta MN2 at medial side of apex of mandible longer than length of retinaculum.

DESCRIPTION. Habitus campodeiform. Cephalic capsule about subequal in length and width or slightly elongated, narrowed at base, with distinct neck. Frontale not reaching hind margin of head; coronal suture distinct. Nasale protruding, with serration. Parietale with 1, 2 or 6 stemmata on each side. Postocular groove absent, cervical groove absent (*Siagona*) or present (*Enceladus*). Frontal sutures weakly (Fig. 3) or normally (Fig. 22) sinuated. Ventral ecdysial suture present. Antenna, maxilla (bearing lacinia), and labium highly modified (see generic descriptions for details). Mandible without penicillus; retinaculum relatively large; cutting edges of terebrum and retinaculum smooth, without serration. Thoracic pleura fused with terga. Mesothorax with proportionally very large spiracles. Legs with two equal claws and markedly developed pretarsus on ventral side between apex of tarsus and base of claws. First abdominal segment with enlarged spiracles, almost as large as those on mesothorax; segments II-VIII with fused ventrites, inner- and outer postventrites. Abdominal segment IX strongly reduced in length; urogomphi separated between themselves by narrow membrane, their bases located near posterior margin of abdominal segment VIII. Pygidium relatively very short. Urogomphi relatively thin and very long, their length about 0.5 - 1.0 X that of remaining body.

Chaetotaxy: highly modified with many primary sensilla absent or their homologization questionable. Frontale with primary pores FRa - FRe and setae FR2, FR3, FR5 - FR7, FR10, FR11; adnasale with group of 10-30 setae, including primary setae FR8 and FR9. Parietale without secondary setae; with pores PAa, PAb, PAc, PAi, PAk, PAm, PAo and setae PA1 - PA3, PA7, PA11 - PA13, PA15, PA16, PA19. Setae PA4 - PA6, PA8, PA14 absent; presence of pores PAf, PAg, PAj questionable. Antennomere I with 3 setae at apex and 4 pores, 2 of them located dorsally at basal third and 2 ventrally near apex; second antennomere with 3 setae apically. Sensorium on antenna absent. Mandible with all primary sensilla, except setae MN1; seta MN2 longer than retinaculum; dorsal surface of mandible with numerous secondary setae. Maxilla with numerous secondary setae and primary sensilla MXa, MXb, MXc, MX5 on stipes and seta MX6 on apex of lacinia; remaining primary sensilla unrecognized. Labium with numerous secondary setae and primary sensilla LA1, LA2, LAb; remaining primary sensilla unrecognized. Thoracic and abdominal chaetotaxy highly modified and many primary sensilla unrecognized. Legs with setae UN1 and UN2 located on pretarsus; tarsus with all primary sensilla except seta TA1; trochanter with setae TR1, TR4 and pores TRf and TRg. Chaetotaxy of ninth abdominal segment, urogomphi and pygidium highly modified, homologization of primary sensilla impossible.

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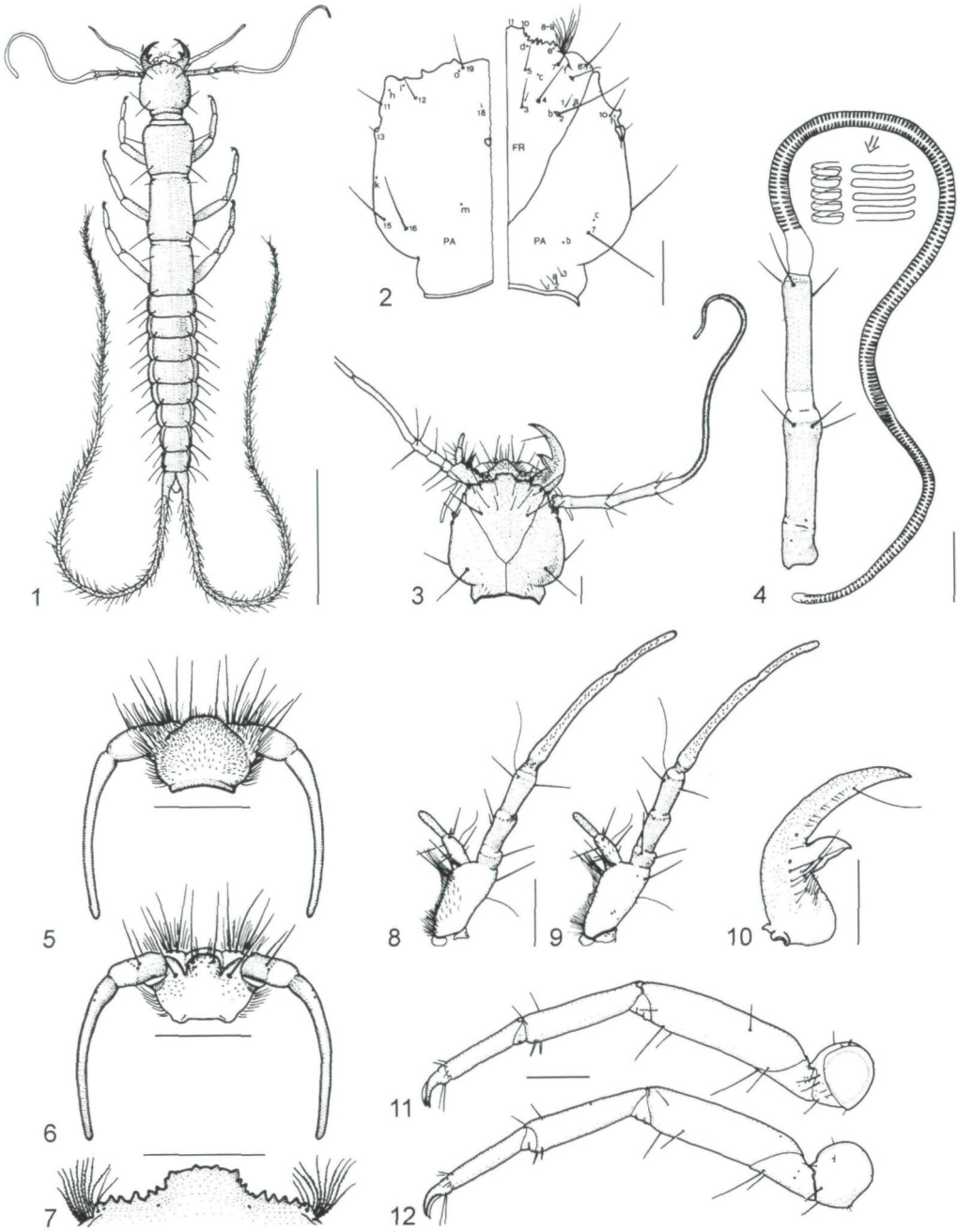

Figs. 1 - 12: Larva of *Siagona* sp., 1) habitus, dorsal view. Scale line = 5 mm. 2) cephalic capsule, ventral (left) and dorsal (right) views; 3) head, dorsal view. Scale lines = 0.5 mm. 4) right antenna, dorsal view; 5 - 6) labium, dorsal (5) and ventral (6) views; 7) nasale, dorsal view. Scale lines = 0.5 mm. 8 - 9) right maxilla, dorsal (8) and ventral (9) views; 10) left mandible, dorsal view; 11 - 12) leg, anterior (11) and posterior (12) views. Scale lines = 0.5 mm.

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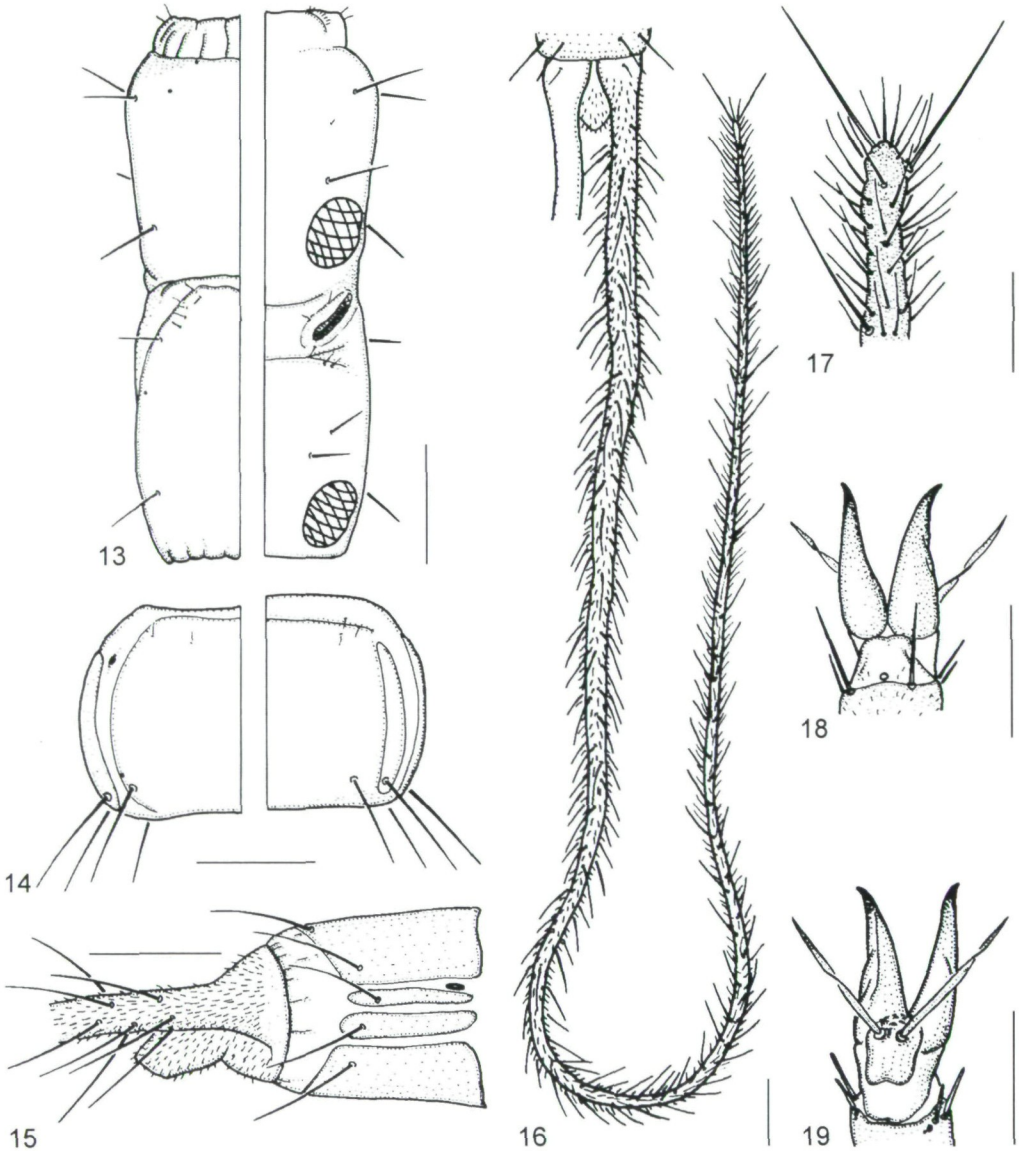

Figs. 13 - 19: Larva of *Siagona* sp. 13) prothorax and mesothorax, dorsal (left) and ventral (right) views; 14) abdominal segment IV, dorsal (left) and ventral (right) views; 15) abdominal segments VIII and IX, base of urogomphi and pygidium, lateral view; 16) abdominal segment IX, right urogomphus and pygidium, dorsal view; 17) apex of right urogomphus, dorsal view; 18 - 19) apex of tarsus and claws, dorsal (18) and ventral (19) views. Scale lines for Figs. 13 - 16 = 0.5 mm; for Figs. 17 - 19 = 0.2 mm.

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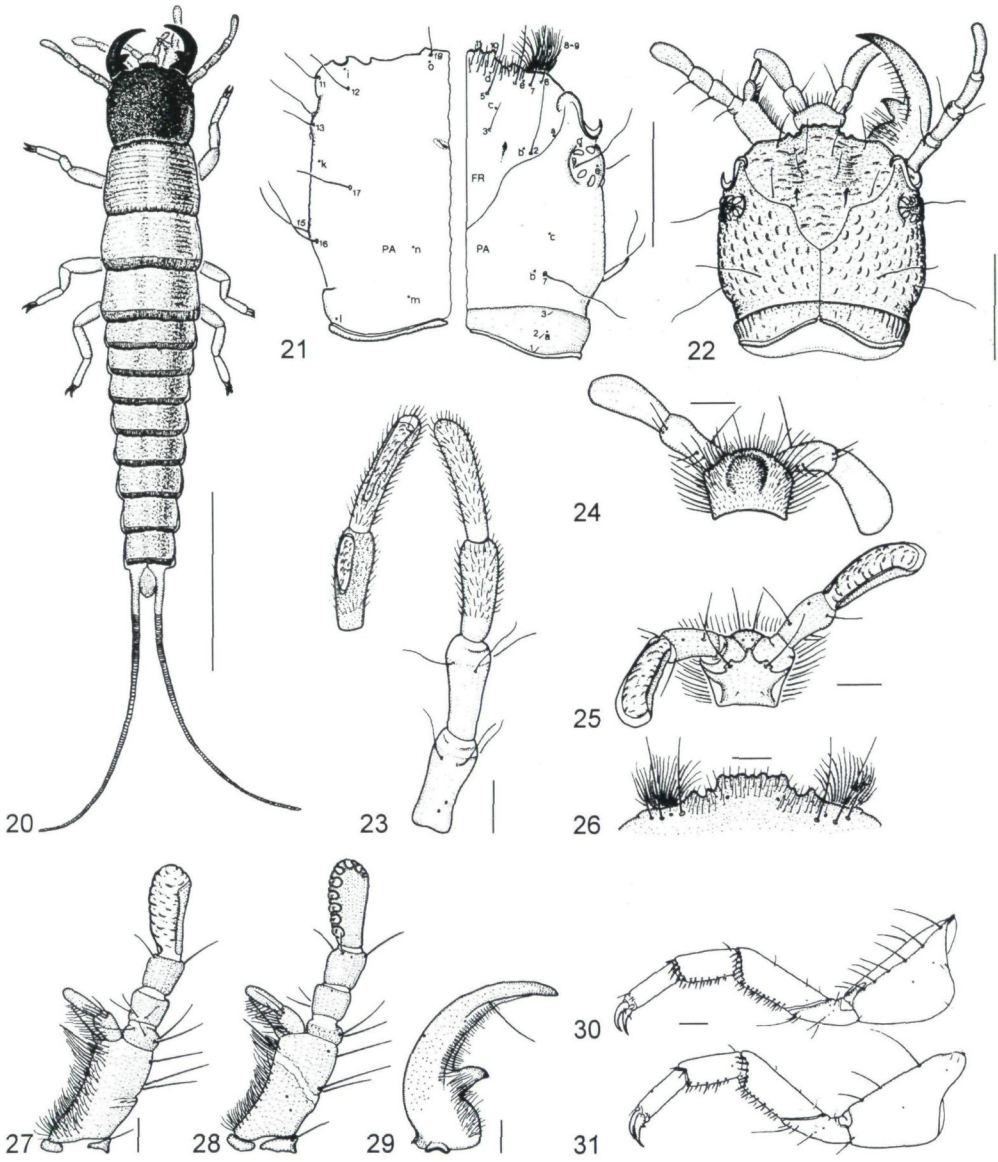

Fig. 20: Larva of *Enceladus gigas*, habitus, dorsal view. Scale line = 10 mm. 21) cephalic capsule, ventral (left) and dorsal (right) views; 22) head, dorsal view. Scale lines = 2.5 mm. 23) right antenna, dorsal view (ventral view for two apical antennomeres); 24 - 25) labium, dorsal (24) and ventral (25) views; 26) nasale, dorsal view. Scale lines = 0.5 mm. 27 - 28) right maxilla, dorsal (27) and ventral (28) views; 29) left mandible, dorsal view; 30 - 31) leg, anterior (30) and posterior (31) views. Scale lines = 0.5 mm. 32) prothorax and mesothorax, dorsal (left) and ventral (right) views; 33) abdominal segment IV, dorsal (left) and ventral (right) views; 34) abdominal segments VIII and IX, base of urogomphi and pygidium, lateral view; 35) abdominal segment IX, right urogomphus and pygidium, dorsal view; 36) apex of right urogomphus, dorsal view; 37 - 38) apex of tarsus and claws, dorsal (37) and ventral (38) views. Scale lines for Figs. 33 - 35 = 1.0 mm; for Figs. 36 - 38 = 0.2 mm.

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Siagona sp.

(Figs. 1 - 19)

DIAGNOSIS. Larvae of the genus *Siagona* are easily recognized within the family by having whip-like antenna (Fig. 4) with apical, flexible, unsclerotized part at least as long as the combined length of all basal sclerotized antennomeres.

DESCRIPTION. Measurement: maximum head width 1.90 mm (n = 1). Color: poorly pigmented, head slightly darker than almost colorless body. Microsculpture absent, cephalic capsule and sclerites smooth. Cephalic capsule divergent posteriorly behind stemmata (Fig. 3), its widest part near basal quarter; neck relatively narrow, about 0.59 X as wide as widest part of cephalic capsule. Length of coronal suture about 0.3 X that of frontale. Cervical groove absent. Frontal sutures weakly sinuated, almost straight (Fig. 3). Frontale about 1.2 X as long as wide. Parietale on each side with 2 poorly developed stemmata in anterior row. Adnasale with denticles (Fig. 7). Antenna about 4 - 5 X as long as mandible (Figs. 3, 4); two-segmented with long, flexible, apical unsclerotized appendage about 2 X as long as both basal sclerotized antennomeres combined; first and second antennomeres subequal in length; first antennomere divided by membranous zone between two dorsal pores in basal third; flexible appendage without sensilla, with internal structure (Fig. 4). Mandible (Fig. 10) without keel on dorsal surface of terebrum. Stipes (Figs. 8, 9) without transversal membranous band; apex of stipes about 1.5 X as wide as base; apical palpomere of maxilla about 1.6 X as long as 3 basal palpomeres combined, membranous, with constriction in apical part, with small teeth-like structures inside. Labium (Figs. 5, 6) directed anteroventrally, labial palpi directed posteriorly; second palpomere membranous, about 3 - 4 X as long as first. Thorax and abdomen (Figs. 13, 14) elongated and relatively narrow; all terga without carina; thorax uniformly sclerotized and sclerites fused together and unrecognized. Legs directed anteriorly (Fig. 1); with elongated femur, tibia and tarsus (Figs. 11, 12); coxa relatively very short, about 0.5 X as long as tibia. Each claw (Figs. 17, 18) without tooth on ventral surface. Abdominal epipleura complete, not divided. Urogomphi (Figs. 1, 16) about as long as remaining body; without pseudosegments.

Chaetotaxy: Setae on cephalic capsule and sclerites of normal thickness and flexibility for carabid larvae (Figs. 2, 13, 14) except for 4 thin and very flexible setae present on head and appendages: one in anterior angles of frontale basally of pore FRf, one at middle of lateral side of stipes, one at middle of basal galeomere, one at apex of maxillary palpomere III. Frontale (Fig. 2) with pore FRf and setae FR1 and FR4; without long secondary seta medially of FRe; with long and thin secondary seta between FR4 and FR6; adnasale with 15 - 17 setae, primary setae FR8 and FR9 unrecognized among them; dorsal surface of frontale near nasale and adnasale without secondary setae (Fig. 7). Parietale (Fig. 2) with setae PA10, PA18 and pores PAh. Setae PA9, PA17 and pores PAn absent; presence of pores PAe and PAl questionable. Antenna (Fig. 4) with about 10 pore-like sensilla on antennomere II apically. Mandible (Fig. 10) with about 30 secondary setae dorsally; pore MNc located at base of terebrum; ventral surface of mandible with 2 pores. Maxilla (Figs. 8, 9) with groups gMX consisting of about 60 - 70 setae; seta MX1 on cardo absent; lateral side of stipes with 2 setae; galeomere I with 8 setae; galeomere II without sensilla; palpomere I with 2 setae and 5 pores; palpomere II with one long and 3 short setae and one pore; palpomere II with 3 setae and one pore; palpomere IV without sensilla. Labium on dorsal surface (Figs. 5, 6) with numerous short setae; lateral surface and area near base of palpi with numerous long setae; palpomere I with 2 setae and about 5 pores near apex, including LAb; palpomere II without sensilla. Thoracic chaetotaxy highly modified and illustrated on Fig. 13, homologisation of sensilla impossible. Coxa (Figs. 11, 12) with 14 setae and 3 pores; trochanter with 2 setae and 6 pores; femur with 6 setae and one pore; tibia with 4 setae and one pore. Setae UN1 and UN2 on pretarsus flat (Figs. 18, 19). Abdominal epipleura and hypopleura each with one long seta posteriorly (Fig. 14). Abdominal segment IX, pygidium and urogomphy (Figs. 15, 16, 17) covered with numerous short setae; urogomphy additionally with numerous relatively long setae.

BIONOMICS. Little is known about the biology of *Siagona*. MOORE (1972) reported that larvae

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were collected in pitfall traps together with adults on wet, heavy clay soils which were slowly drying out. He proposed that, quite likely, siagones inhabit the deep cracks in drying mudflats. LACORDIER (1977) dissected numerous adult specimens and found cuticular remnants in digestive tracts. ZETTO BRANDMAYR & PIZZOLOTTO (1994) published some biological data concerning *Siagona europea* DEJEAN, 1826 from southern Italy and proposed that adults feed almost exclusively upon ants; they were unable to rear larvae in captivity. I collected adults of *S. europea* in Turkmenia in horizontal cracks under drying clay along saline streams in semi-desert areas, but I have not been able to obtain larvae under laboratory conditions. Adults lived in captivity for two months without laying eggs.

REMARKS. MOORE (1972) described a larva of *Siagona* and arbitrarily identified it as *S. brunnipes* DEJEAN, 1825. However, LACORDIER (1977: 627; 1978: 161, 164; 1980: 78), doubted the identification and proposed *S. mandibularis* GUÉRIN-MÉNEVILLE, 1838 as the most probable candidate for the described larva. The previously published description was based on a single specimen with a head width of 4 mm; two more specimens with a head width of 2 mm were available but not described. Our study is based on one of those two smaller larvae which belongs, according to MOORE (1972), to another species of *Siagona*. This is likely the case since there are some differences between the specimen studied and the one described by MOORE (1972). Moore's specimen has one stemma on each side of cranium instead of two and lacinia with two setae at apex instead of one.

It should be mentioned also that according to MOORE (1972) larvae of *Siagona* have four-segmented antennae and the apical segment is exceedingly long and slender, whip-like. The present comparison of larvae of *Siagona* with those of *Enceladus* showed that *Siagona* has only two true basal antennomeres (Fig. 4) and that the first one is divided by a basal membranous zone between two dorsal pores. This view is supported by the identical antennal chaetotaxy in *Siagona* (Fig. 4) and *Enceladus* (Fig. 23). Subsequently I believe that the long flexible apical whip-like unsclerotized antennal appendage in *Siagona* is homologous to third and fourth antennomeres of *Enceladus* larva.

The following autapomorphic features are recognized for *Siagona*: 1) cephalic capsule with narrow neck; 2) parietale with one or two stemmata in anterior row; 3) antenna 2-segmented with a long, flexible, whip-like appendage about 2 X longer than both antennomeres combined; 4) basal antennomere divided by membranous zone; 5) fourth palpomeres of maxilla and second one of labium relatively long and unsclerotized; 6) thorax and abdomen elongated and relatively narrow; 7) legs directed anteriorly; 8) coxa relatively very short; 9) parietale without primary sensilla PA9, PA17 and PAn; 10) antennomere 2 with about 10 pore-like sensilla apically; 11) cardo without seta MX1; 12) setae UN1 and UN2 on pretarsus flat; 13) abdominal segment IX, pygidium and urogomphy with numerous setae.

Enceladus gigas BONELLI, 1813

(Figs. 19 - 38)

DIAGNOSIS. Larvae of *Enceladus gigas* are recognized within the family by having membranous zones on antennomeres III and IV (Fig. 23), and on last maxillary (Figs. 27, 28) and labial (Figs. 24, 25) palpomeres.

DESCRIPTION. Measurement: maximum head width of 5 specimens 4.50 mm, 4.75 mm, 4.85 mm, 5.59 mm, 6.65 mm. Color: cephalic capsule, mandibles, and caudal margins of thoracic and abdominal segments black, remaining body reddish-brown. Microsculpture: cephalic capsule with markedly developed microsculpture all over; frontale on each side with short keel between setae FR2; protergum dorsally with transversal cuticular folds, those on meso- and metatergum relatively less developed. Cephalic capsule parallel-sided behind stemmata (Fig. 22), its widest part at middle; neck relatively wide, about 0.83 X as wide as widest part of cephalic capsule.

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Length of coronal suture about 0.5 X that of frontale. Cervical groove present, forming kind of transverse keel reaching dorsally cervical suture, not prolonged upon ventral side. Frontal sutures markedly sinuated (Fig. 22). Frontale about 1.2 X as wide as long. Parietale with 6 markedly developed stemmata on each side deposited in anterior and posterior rows. Adnasale without denticles (Fig. 26). Antenna about 1.3 X as long as mandible (Figs. 22, 23); 4-segmented; without flexible terminal appendage; all 3 basal antennomeres subequal in length, fourth about 1.3 - 1.4 X as long as first; antennomere I complete, not divided by membranous zone; antennomeres III and IV with membranous area on ventral surface. Mandible (Fig. 29) with keel on dorsal surface of terebrum. Stipes (Figs. 27, 18) with transverse membranous band ventrally at middle; apex of stipes about same width as base; apical palpomere of maxilla about as long as three basal palpomeres combined, with large membranous area, without constriction, without internal teeth-like structures. Labium (Figs. 24, 25) directed antero-ventrally, labial palpi directed anteriorly or posteriorly; palpomere II with large membranous area, about 2 X as long as first. Thorax and abdomen not elongated; all terga, except that on prothorax, with distinct carina (Figs. 20, 32, 33). Thoracic sclerotisation (Fig. 32) less modified than in *Siagona*: prothorax with free (recognizable) prosternum and episternum, meso- and metathorax with free episternum and median sternum bearing setae MS3. Legs directed laterad (Fig. 20); with segments of normal length (Figs. 30, 31); coxa about 2 X as long as tibia. Each claw (Figs. 37, 38) with tooth-like process on ventral surface at basal third. Abdominal epipleura (Fig. 34) divided into three parts: relatively large central and two smaller anterior and posterior. Urogomphi (Figs. 20, 35) about half as long as body; with pseudosegments (Fig. 36).

Chaetotaxy: Setae on cephalic capsule and sclerites thinner and more flexible than usual for carabid larvae (Figs. 21, 32, 33); 4 very thin and flexible setae on head and appendages noted for *Siagona* absent in *Enceladus*. Frontale (Fig. 21) without pore FRf and setae FR1 and FR4; with long secondary seta medially of FRe; without long and thin secondary seta between FR4 and FR6; adnasale with about 30 setae, primary setae FR8 and FR9 unrecognized among them (Fig. 26). Parietale (Fig. 21) with setae PA9, PA17 and pores PAd, PAe PAl and PAn. Setae PA10 and PA18 absent; presence of pore PAh questionable. Antenna (Fig. 23) without pore-like sensilla on antennomere II apically; antennomeres III and IV with numerous short setae. Mandible (Fig. 29) with about 80 secondary setae dorsally; pore MNc located at middle of terebrum; ventral surface of mandible without pores. Maxilla (Figs. 27, 28) with setal group gMX consisting of about 90-100 setae; seta MX1 on cardo present; lateral side of stipes with 3 setae; galeomere I with about 20 setae; galeomere I with 9 setae; palpomere I with 4 setae and about 7 pores; palpomere II with 3 setae and one pore; palpomere III with 3 setae and one pore; palpomere IV without sensilla. Labium on dorsal and lateral surface (Figs. 24, 25) with numerous short and long setae; palpomere I with 5 setae and pore LAb near apex; palpomere II without sensilla. Thoracic chaetotaxy highly modified (Fig. 32), homologisation of sensilla impossible. Coxa (Figs. 30, 31) with 16 setae and 4 pores; trochanter with 8 setae and 5 pores; femur with about 40 setae and one pore; tibia with about 20 setae and one pore. Setae UN1 and UN2 on pretarsus not flat (Figs. 37, 38). Abdominal epipleura (Fig. 34) with 2 long close setae at posterior part of cental sclerite; hypopleurites without setae. Abdominal segment IX, pygidium and urogomphy (Figs. 34, 35, 36) not covered with short setae; urogomphy with 7 relatively long setae.

BIONOMICS. Erwin & Sims (1984: 368) reported that adults of *Enceladus gigas* live under bark of large trees. Larval habitat is unknown; some of the studied larvae were collected dead on soil surface.

REMARKS. The following autapomorphic features are recognized for *Enceladus*: 1) cervical groove forming kind of transverse keel reaching dorsally cervical suture; 2) stipes with membranous bend at middle; 3) each claw with a tooth on ventral surface at basal third; 4) abdominal epipleura transversely divided into relatively large central and two smaller anterior and posterior plates; 5) setae on cephalic capsule and sclerites thin and flexible; 6) frontale without

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pore FRf and setae FR1 and FR4, with long secondary seta medially of FRe; dorsal surface of nasale and adnasale with about 30 relatively short secondary setae on each side; parietale without setae PA10 and PA18; 7) abdominal epipleura with 2 long closely located setae at posterior part of central sclerite.

Discussion

For a long time the supertribe Siagonitae included, in addition to Siagonini and Enceladini, the tribe Cymbionotini with a single Afro-Asiatic genus *Cymbionotum* BATES, 1874 (KRYZHANOVSKIJ 1976, 1983, ERWIN 1978, 1979). ERWIN (1978) indicated some apomorphic character states between *Cymbionotum* and the remaining genera based on adults morphology. Later, however, it was recognized that the genus *Cymbionotum* is actually unrelated to Siagonitae (ERWIN 1985) which was supported by the discovery and study of previously unknown larvae of *Cymbionotum* (Grebennikov & Bousquet, unpublished).

Morphological characters of *Siagona* and *Enceladus* larvae support their sister-group relationship based on a number of synapomorphies. Three of them were discovered by ERWIN (1978): 1) extremely long urogomphi; 2) absence of penicillum; and 3) absence of seta MN1 ("scrobal" seta in ERWIN 1978) on mandible. The following synapomorphies can be added: 4) cephalic capsule with distinct neck-part; 5) retinaculum relatively large and similarly shaped; 6) some thoracic and abdominal sclerites fused together; 7) mesothorax and first abdominal segment with very large spiracles; 8) ninth abdominal segment stronlgy reduced in length; 9) adnasale with a group of 10 - 30 setae; 10) numerous primary setae and pores absent; 11) seta MN2 extremely long; 12) Antennomeres I and II, mandible, maxilla and labium with numerous secondary setae.

One additional character state of *Siagona* and *Enceladus* larvae should be discussed. I believe that larvae share an apomorphic modification of two apical antennomeres and apical maxillary and labial palpomeres. This character can be named as desclerotization and elongation of apical segments of cephalic appendages instead of having them normally sclerotized and of normal length. In *Siagona* apical maxillary and labial palpomeres lost sclerotization and became very long flexible membranous projections (Figs 5, 6, 8, 9); in *Enceladus* they have strongly reduced incomplete sclerotization and are markedly enlarged (Figs 24, 25, 27, 28). In *Siagona* the antenna is two-segmented and terminated by a flexible whip-like structure apparently homologous to antennomeres III and IV (Fig. 4); in *Enceladus* the antenna is four-segmented, but both apical antennomeres have a markedly developed unsclerotized area (Fig. 23) along themselves. Consequently, I believe that the unsclerotized areas in *Enceladus* larvae represent a first step towards the highly modified unsclerotized structures in *Siagona*. If this hypothesis is correct, the supertribe can be characterized by one more apomorphic feature apparently unique within the family Carabidae.

The relationship of the group is uncertain. JEANNEL (1946: 206) proposed Promecognathitae as an adelphotaxon to Siagonitae without providing reasons; such hypothesis was not supported by larval morphology (see BOUSQUET & SMETANA 1986). Other likely candidats were proposed by ERWIN (1978), namely Scaritini or Broscini. I am unable to comment on this hypothesis since known Siagonitae larvae are highly modified and have little in common with those of Scaritini and Broscini.

Conclusions

Some points of the present study should be emphasized. Known larvae of the supertribe Siagonitae are among the most highly modified larvae within the family Carabidae. A number of larval synapomorphies have been discovered to support the monophyly of the supertribe and each of the genera is characterized by numerous autapomorphies; however no evidence has been found to clarify the relationship of the supertribe. A study of additional larval Siagonitae is needed in order to improve the proposed tentative description and diagnosis of the supertribe. Discovery of

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Siagonella and particularly *Luperca* larvae will be of a great interest since the hypothesis about similar modifications of apical articles of cephalic appendages could be critically examined.

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