

Revision of the family Omalidae (Coleoptera, Elateroidea)

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The taxonomic revision of the Palearctic beetle family Omalidae is presented. The morphology of the family is described in detail and the relationships of genera are discussed. The genus *Thilmanus* Gemminger, 1869 is classified in Omalidae and the subfamily Thilmaninae Kazantsev, 2005 described in Lycidae for *Thilmanus* is considered redundant in Omalidae. The subgenus *Phaeopterus* Costa, 1857 is elevated to the genus level. *Omalisus (Phaeopterus) minutus* Pic, 1938 is proposed to be a junior subjective synonym of *Phaeopterus unicolor* Costa, 1857. *Thilmanus longicollis* var. *laticeps* Pic, 1913 from Southern France is elevated to the full species status, *Thilmanus longicollis* Pic, 1912 from Sardinia is proposed to be a junior subjective synonym of *T. obscurus* Baudi, 1872. *Omalisus (Phaeopterus) nigricornis* Reitter, 1881 is excluded from Omalidae and placed in *Euanoma* Reitter, 1889 in Drilidae. *Omalisus (Phaeopterus) flavangulus* Späth, 1898 is proposed to be a junior subjective synonym of *E. nigricornis* Reitter, 1881. In total, eight species classified in three genera are recognized in Omalidae. Redescriptions of all Omalidae genera are provided. Each species of the family is presented with a diagnosis, full description, illustrations of male genitalia and a comprehensive bibliography. Extensive data on distribution of all species is provided and the distributions of genera and the species groups are discussed. A key to all Omalidae species and genera is included and fully illustrated.

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Introduction

The Omalidae, one of the smallest beetle families, is classified in the superfamily Elateroidea in relationship with other soft-bodied families earlier classified as Cantharoidea (Crowson 1972, Lawrence 1988, Lawrence and Newton 1995). Recently, Bocakova *et al.* (2007) proposed a relationship between Omalidae, Drilidae and Elateridae using four molecular markers. Altogether twelve species were classified in omalids and all of them were reported from restricted ranges in the Mediterranean, Central and Western Europe (Bocak 2007). Although Omalidae occur in areas with a long history of entomological research, due to the rareness of all species, except *Omalisus fontisbellaquaei* Fourcroy, 1785 our knowledge about their taxonomy, biology and distribution is very limited and the classification and zoogeography of Omalidae needs thorough revision.

History of Omalidae classification: *Omalisus fontisbellaquaei* (Geoffroy 1762, 1785) was the first species of Omalidae described and long remained the only known representative of the family. Only later did Laporte (1840), Mulsant, (1852), Costa (1857), Baudi (1872), Reitter (1881), and Späth (1898) describe further species of Omalidae from Southern Europe. All descriptions were very short, often uninformative and without differential diagnoses which would enable reliable identification. Later in the 20th century, Pic (1901, 1912, 1913) and Lesne (1921) described a few additional species: *O. nicaeensis* Lesne, 1921, *O. (Phaeopterus) graecus* Pic, 1901, *Thilmanus longipennis* Pic, 1912, and *Thilmanus longipennis* var. *laticeps* Pic, 1913. These descriptions remained the last contribution to the alpha taxonomical knowledge of Omalidae for a long time. Recently, during revision of some drilid gen-

era, Kundrata & Bocak (2007) transferred one species originally classified in *Omalisus* Geoffroy, 1762 to the genus *Euanoma* Reitter, 1889 in Drilidae.

Lacordaire (1857) proposed the family group name "Omalisides" within his "Malacodermes" for three species of *Omalisus*. Later, Bourgeois (1882) was the first author who tried to summarise the actual knowledge of Omalisidae and to propose a hypothesis about their relationships to other elateroid families. He considered Omalisidae to be a part of Lycidae, but mentioned some characters that Omalisidae shared with Elateridae. Lycidae were cited as a tribe "Lycides" in the family "Malacodermes" and they were subdivided in two subtribes "Homalisides" and "Lycides vrais". Bourgeois classified three genera in Homalisides: *Omalisus* Geoffroy, 1762, *Thilmanus* Gemminger, 1869, and *Paradrilus* Kiesenwetter, 1866; the last genus was transferred to Drilidae (Hicker 1925). Bourgeois (1894) segregated *Omalisus* to a group of equivalent status to Lycidae or Cantharidae. Kleine (1933, 1942) followed the traditional view on the position of Omalisidae and classified omalids as a subfamily within Lycidae in his world catalogue and in the review of the lycid Palaearctic fauna. Kleine (1942) compiled keys and redescrptions of all known species of Omalisidae, but as he had never seen most species and based many of his redescrptions only on information available in literature, the value of his study is very limited. He listed in his studies four omalid genera: *Omalisus* (including the subgenus *Phaeopterus*), *Euanoma* Reitter, 1889, *Pseudeuanoma* Pic, 1901 and *Thilmanus*. The family status was given to Omalisidae by Crowson (1955) and since that time the family status of Omalisidae has been generally accepted (Crowson 1972, 1981, Lawrence and Newton 1995). Crowson (1972) revised the classification of Cantharoidea and he transferred *Pseudeuanoma* to Drilidae and *Thilmanus* to Lycidae. As this author did not study *Euanoma*, it is only mentioned as a possibility that some other genera can be classified in Drilidae without further specification. The position of *Thilmanus* remains contentious. *Thilmanus* was returned to Omalisidae by Bocak & Bocakova (1990) on the basis of male genitalia morphology and later *Thilmanus* was classified in Drilidae by Medvedev & Kazantsev (1992) on the basis of the allegedly sclerotized tentorium and presence of the elytral epipleuron (opposing Crowson 1972). Kazantsev (2005)

transferred *Thilmanus* to Lycidae when he found the non-connected ventral arms of tentorium in *Thilmanus* and he described the subfamily Thilmaninae which was placed in Lycidae in close relationship with the lycid neotenus groups.

The aims of this study are to revise the classification and distribution data of Omalisidae and to provide comprehensive information on the morphology of this group as a firm basis for their classification and further evolutionarily oriented research. The ontogeny of many elateroid lineages is modified (Crowson 1972, 1980, Cicero 1988, Bocakova *et al.* 2007). In Omalisidae, all females are proved (*O. fontisbellaquaei*) or expected (other species) to undergo the incomplete metamorphosis and they remain wingless and physogastrous when mature. Their relationships with other elateroid families can elucidate the evolution of neoteny in this group. Most species of Omalisidae were not collected for decades and they were omitted from the recent studies on elateroid soft-bodied beetles (Cicero 1988, Kazantsev 2005). As they are not available for molecular studies and the morphology of male adults remain the only source of phylogenetic information, this study should produce further morphological data for studies on the elateroid phylogeny. Additionally, the winglessness of females strongly limits their capability to disperse and therefore these animals are among the most interesting paleogeographical indicators.

Material and Methods

The revision is based on the male adult stage of omalids and the material was obtained from major collections either housing the type material of Omalisidae or historically having valuable collections of insects from the Mediterranean or the Balkan. All examined material is cited with the full original locality data under the appropriate species. Due to the rareness of almost all species of Omalisidae, the total number of specimen studied is small compared with similar studies of other groups. Even major European collections do not house in most cases, other species than the widespread *Omalisus fontisbellaquaei*.

The detailed morphology of the type species of the family, *Omalisus fontisbellaquaei*, was described and selected morphological structures were illustrated. Male genitalia were dissected and illustrated for each species. The apical part of the abdomen was removed when the male genitalia

were dissected and it was boiled briefly in 10% aqueous potassium hydroxide. The genitalia were then extracted from the tip of abdomen and embedded in glycerol. Illustrations of all morphological structures were derived from photographs taken with a digital camera attached to a stereoscopic microscope. Body length of all available specimens was measured and the intervals between minimum and maximum value were given in descriptions along with the number of measured specimens. Further morphometric data were taken from one randomly selected adult male for each species with an ocular grid using the Olympus SZX-12 binocular dissecting microscope. The following measurements were taken: BL – The body length, measured from the fore margin of the head to the apex of the elytra; WH – The width of the humeri measured at the point where elytral edges become parallel-sided; PW – The width of the pronotum, measured at the widest point, usually at the base of pronotum; PL – The pronotum length at the midline; Edist – The minimum frontal distance between the eyes; Ediam – The maximum eye diameter in the lateral view.

Material was examined from the following institutions and collections:

- DEIC – Deutsches Entomologisches Institut, MÜNcheberg, Germany
 MHNP – Museum d' Histoire Naturelle, Paris, France
 NHMW – Naturhistorisches Museum, Wien, Austria
 MZMB – Moravske Zemske Muzeum, Brno, Czech Republic
 MGCB – Michael Geiser Collection, Basel, Switzerland
 RCSL – Robert Constantin Collection, Saint Lo, France
 NHMB – Natural History Museum, Budapest, Hungary
 NHMP – Natural History Museum, Prague, Czech Republic
 ZMBC – Zoological Museum of the Humboldt University, Berlin, Germany
 LMBC – Collection of Ladislav Bocak and Milada Bocakova, Olomouc, Czech Republic

Taxonomy

Family Omalidae Lacordaire, 1857

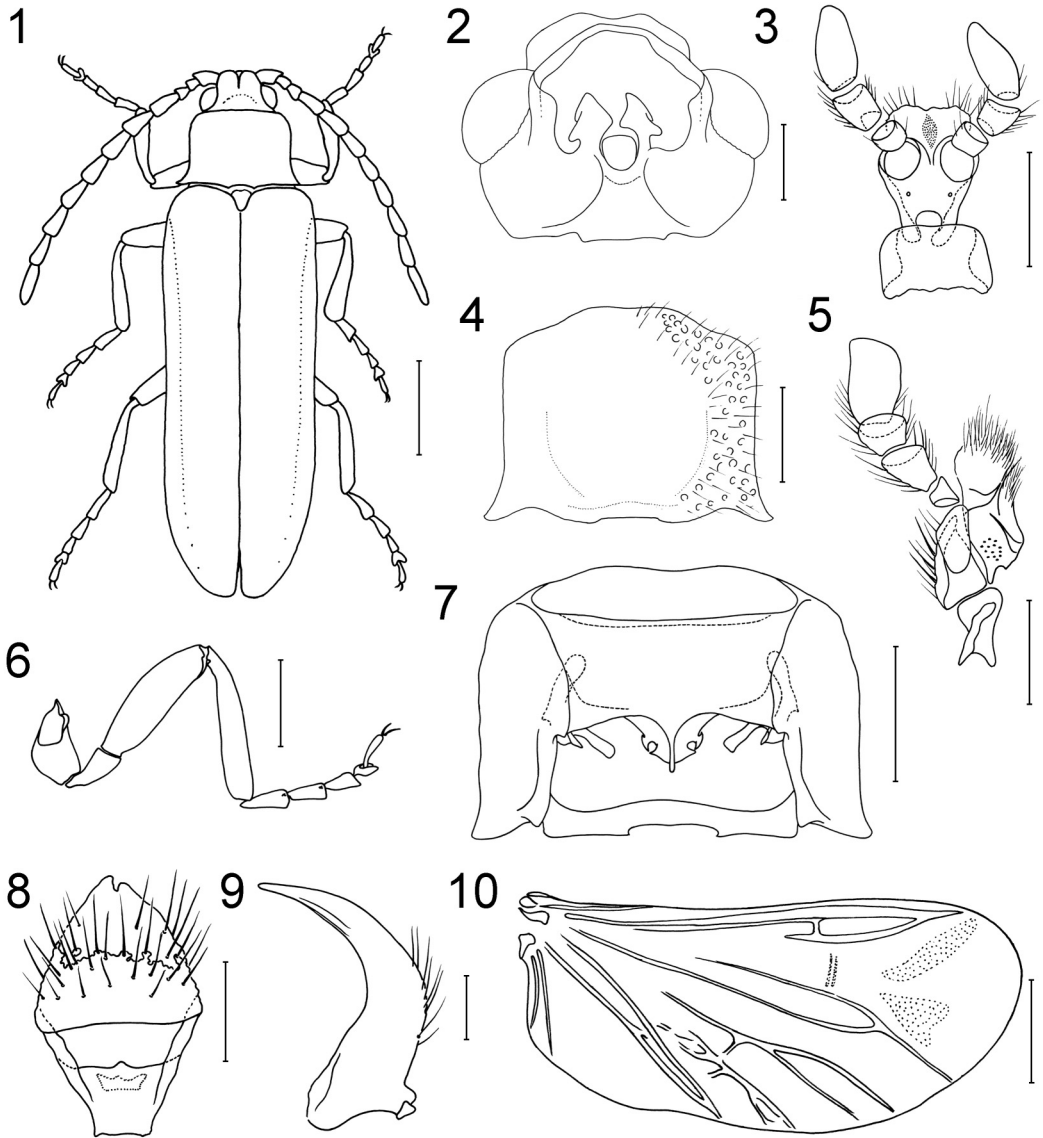
Homalidae Lacordaire, 1857: 303 (based on unjustified emendation).

Type genus. – *Omalisus* Geoffroy, 1762.

Diagnosis. – Male adults of Omalidae resemble in some aspects several elateroid families, such as

Drilidae (*Euanoma* Reitter, 1889, *Pseudeuanoma* Pic, 1901), Cerophytidae (*Cerophytum* Latreille, 1809), and Elateridae (especially some genera from the subfamily Denticolinae, such as *Campylomimus* G. Müller, 1960 and *Denticollis* Piller & Mitterpacher, 1783). They are easily separated from Elateridae by several characters, such as the lightly sclerotized body, the absent long prosternal process, and the well developed longitudinal keels at the lateral margins of the pronotum (only *Omalisus* and *Phaeopterus*). They differ from Cerophytidae by the flat pronotum, filiform antennae and less protruding frons. Drilidae and Omalidae cannot be simply distinguished by any clear character which would be present in all representatives. *Omalisus* and *Phaeopterus* have the well developed elytral cells and the longitudinal keels at the lateral margins of pronotum both of which unknown in Drilidae. Drilidae either have the similar relatively long prosternum (*Euanoma* and *Pseudeuanoma*) or the prosternum is much shorter (*Drilus*, *Malacogaster*, *Paradrilus*, and *Selasia*). The omalid genus *Thilmanus* differs substantially in general appearance from *Omalisus* and *Phaeopterus*. Its body is small and very lightly sclerotized. It resembles in general appearance some small bodied Cantharidae (e.g., some *Malthinus* Latreille, 1806 or *Malthodes* Kiesenwetter, 1852), from which it can be separated by the shape of pronotum (Fig. 26) and the male genitalia (Figs 36–38). *Thilmanus* differs from Lycidae where it was sometimes classified by the absence of any median longitudinal keel on pronotum, seven ventrites in the abdomen, and male genitalia which do not resemble any type known in Lycidae (Figs 36–38).

General structural description of the adults of Omalidae (Figs 1–38). – Adult, male. Moderately sclerotized beetles (*Omalisus*, *Phaeopterus*) or cuticle on elytra and abdomen very soft, flexible (*Thilmanus*). Body form elongate, dorso-ventrally flattened, parallel-sided (Fig. 1). Length 3.0–9.0 mm. Some species concolorous and dark (*P. unicolor* Costa, 1857, *Thilmanus* spp.), sometimes with brightly colored elytra (several South European *Omalisus* species with reddish brown elytra) or light brown lateral elytral margins (*O. fontisbellaquaei*). Vestiture sparse, long, moderately erect; most body parts shiny, pronotum and cranium with rough sculpture. Head small, much narrower than prothorax; prognathous, exposed from above, with



Figs 1–10 *Omaliscus fontisbellaquaei*, male. 1. General appearance; 2. Cranium, ventrally; 3. Labium; 4. Pronotum; 5. Maxilla; 6. Hind leg; 7. Prothorax, ventrally; 8. Labrum; 9. Mandible; 10. Hind wing. Scale = 1 mm (Fig. 1, 10); scale = 0.5 mm (Figs 4, 6, 7); scale = 0.25 mm (Figs 2, 5) scale = 0.1 mm (Figs 3, 8, 9).

fully developed mouthparts; head prolonged anteriorly, antennal sockets large, with long, deep groove between them, antennal insertions widely separated, fronto-lateral (Fig. 2). Eyes lateral, strongly hemispherically prominent (*Omaliscus*) or somewhat flat (*Thilmanus*), with coarse facets, eye

diameter distinctly less than their frontal distance. Antennae with 11 antennomeres, round in cross section (Figs 18–20). Scape robust, pear-shaped, slightly asymmetrical; pedicel and antennomere 3 subequal, shorter than antennomere 4. Following antennomeres gradually shortened except terminal

one. All antennomeres with moderately dense, erect pubescence. Fronto-clypeal suture absent; anterior edge of frontoclypeus concave, labrum membranous apically (Fig. 8), with long dense setae at apex. Mandibles long, robust, considerably curved; incisor edge simple, without any teeth (Fig. 9). Maxilla with fused galea and lacinia (Fig. 5). Maxillary palpi four-segmented, apical palpomere parallel-sided, obliquely cut at apex, with short dense pubescence (Fig. 5). Labium small, slender, without ligula, labial palpi tiny, three-segmented (Fig. 3). Pronotum apparently narrower than elytra, flat, with rough structure; medial part shiny in *Omalisus* (Fig. 4), whole pronotum uniformly structured in *Thilmanus* (Fig. 26). Anterior edge almost straight, anterior angles distinct, slightly rounded, laterally bisinuate; posterior angles projecting, acute; posterior edge simple, straight. Partly obtuse (*Omalisus*) or very sharp (*Phaeopterus*) longitudinal keel at margins of pronotum, seldom inconspicuous vestiges of keel present in *Thilmanus*. Scutellum triangular to parallel-sided, simply rounded at apex (Fig. 27). Prosternum robust, prosternal process long, very slender in *Omalisus* and *Phaeopterus* (Fig. 7), shortened in *Thilmanus*, mesoventrite transverse, its frontal margin straight, simple (Fig. 22). Metaventricle with strong keel-shaped anterior process, coxae attached in deep excavations laterally. Metendosternite with simple, robust stalk, arms absent (Fig. 22). Elytra parallel-sided, flattened (Fig. 1). Each elytron with nine longitudinal costae; rounded, partly irregular cells in simple rows between costae (*Omalisus*, *Phaeopterus*); cells inconspicuous and irregular in *Thilmanus*. Costa 6 much stronger than remaining, elevated, forming humeral edge. Legs slender, moderately flattened, slightly sclerotized, densely pubescent (Fig. 6). Coxae well separated, slightly elongate; trochanters slender, obliquely attached to femora, femora slender, long; tarsi with five slender tarsomeres, tarsomeres 1-3 subequal, tarsomere 4 very short, deeply emarginate, tarsomere 5 slender, long (Figs 6, 17). Claws simple. Abdomen with seven free ventrites, terminal male segments as in Fig. 23. Aedeagus of trilobate type, with long parameres (Figs 28-32, 34-38); apices of paramerae curved outward in *Omalisus* (Figs 28-32), membranous in *Phaeopterus* and *Thilmanus* (Figs 34-38); internal sac inconspicuous, membranous, in a few species with slender sclerotized rod (Figs 29-31).

Adult, female: Body moderately robust, feebly sclerotized, abdomen physogastrous (Fig. 11). Head small, without median longitudinal groove (Fig. 12), mouthparts adult like, well developed, mandibles strong, curved. Antennae with 11 antennomeres, robust, antennomeres 4-10 gradually shortened (Fig. 19). Pronotum rounded frontally, with rectangular posterior angles, without lateral longitudinal keels, roughly punctuated at lateral and frontal margins (Fig. 14). Meso- and metathorax modified, pleural part larviform, sternites and tergites simplified (Figs 13, 24). Elytra and hind wings vestigial, elytra with vestigial costae and punctuation, punctures irregular (Fig. 24). Legs flat, shortened (Fig. 13). Ovipositor slender, with long, rod-like baculi (Fig. 25).

Larvae: Only larva of *Omalisus fontisbellaquaei* is known (Bertkau 1891, Burakowski 1988). Length 10-13 mm, slender, about 2 mm wide.

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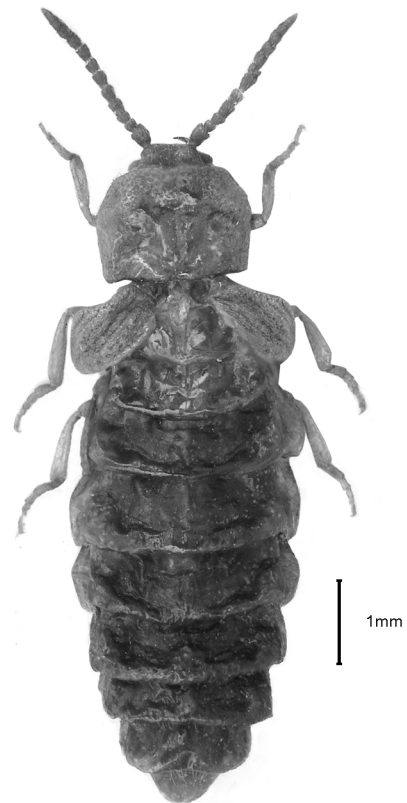


Fig. 11. *Omalisus fontisbellaquaei*, female. General appearance. Scale = 1 mm.

Tergites dark brown, well sclerotized, with rough surface. Sternites pale, feebly sclerotized. Head wider than long, anterior edge prolonged forming slender lobe which is sclerotized basally, almost membranous apically, slightly emarginate at apex. Mandibles slightly longer than labrum, slender, moderately curved at apex. Maxilla well developed, stipes robust, elongate, galea small, pointed anteriorly, lacinia elongate. Maxillary palpi with four palpomeres. Labium elongate with well developed transversal submentum, elongate mentum and subtrapezoidal praementum. Labial palpi with 2 palpomeres. Antennae slender, with three palpomeres, palpomeres 1 and 2 cylindrical, robust, apical one tiny. Pronotum almost rectangular, with both anterior and posterior angles rounded. Remaining tergites except terminal one similar in shape, with rounded finely dentate lateral margins. Thoracic and abdominal terga I-VIII with longitudinal keel and oval, shiny elevations on each side. Tergum IX rounded laterally, without keel. Tergum X elongate and conical, with retractile, membranous, multilobed grooming organ. Legs relatively long, densely setose. Pupae. Unknown.

Biology and Ecology. – The biology of Omalidae is little known, as these beetles have been rarely collected. Of the nine species included here, only one, *O. fontisbellaquaei*, is known from its larval stage and from the female sex. All remaining species are known only in the male adult stage. Omalidae live in deciduous forests of the temperate zone or Mediterranean shrub habitats. Adult males appear in the late spring and early summer, they are capable of flight, but they are usually sitting motionless on leaves in the lowest forest stratum, in shaded situations. Males can be collected by sweeping the herb stratum. Only the biology of *O. fontisbellaquaei* was studied in detail. The female of this species has only vestigial elytra and hind wings (Bourgeois 1882, Bertkau 1891, Geisthardt, 1977), remains in surface soil layers, and can be collected by sifting (Burakowski, personal information). Until now, very few females were collected due to their cryptic way of life. The females of other species are unknown and they are supposed to exhibit neotenic traits similar to *O. fontisbellaquaei*. Larvae of *Omalisus fontisbellaquaei* prey on millipedes (*Glomeris* sp.) (Burakowski 1988). The prey of other species is unknown. Short notes on the omalid biology

were given by Bourgeois (1882). Bertkau (1891) reported luminosity of the larva of *Omalisus fontisbellaquaei* and his finding was mentioned even in recent publications (e. g. Beutel 1995). The luminosity was not confirmed by Burakowski (1988) who recently collected larvae of *Omalisus* in relatively high numbers. Most species are extremely rare and even the biggest collections house only a few specimens of the family usually collected in 19th century. Although *Thilmanus obscurus* Baudi, 1872 is usually another best represented species of the family in most collections, we have not found any *Thilmanus* collected after 1905 regardless of the fact that the group occurs in the areas of quite intensive collecting activity. Similarly, we know of only single recent record of *Phaeopterus*. Only a few *Omalisus* specimens were collected in Southern Europe after World War II.

Distribution. – Omalidae are not only one of the smallest beetle families but they also have a restricted distribution in Europe. They occur in Western and Central Europe from the Atlantic coast to North Eastern Poland, Ukraine, and Romania (only *O. fontisbellaquaei*) and further in Southern Europe from the French Mediterranean coast through Italy to the Balkan Peninsula and Western Turkey. The highest species diversity is located in the southern part of the range. All genera and most species occur along the Mediterranean coast and on the large West Mediterranean islands: *Omalisus* (4 species), *Phaeopterus* (1 species), and *Thilmanus* (2 species). Only *Omalisus* has a very extensive range which corresponds almost with the range of the whole family; *Omalisus fontisbellaquaei*, the most northerly distributed species, is also the only widespread species in the family. Other genera as well as all remaining species are reported having a very restricted range, which probably corresponds with Pleistocene refugia. Similar distribution patterns were reported in the neotenic coleopteran family Drilidae (Kundrata & Bocak 2007). *Phaeopterus* occurs along western coast of Italy (Salerno, Roma, Naples, and the Elba Island) and Corsica; *Thilmanus* in Sardinia, Corsica and the Mediterranean coast of France; *Omalisus* in the Northern Mediterranean; *O. victoris* Mulsant, 1852 in the Maritime Alps; *O. nicaeensis* Lesne, 1921 in the vicinity of Nice in Southern France; *O. taurinensis* Baudi, 1872 in Northwestern, Central and

Southern Italy, and *O. sanguinipennis*, Laporte, 1840 in North Eastern Italy, Croatia and Bosnia Herzegovina. The striking fact is that the ranges of all species are non-overlapping and we did not find any locality where two species of *Omalisus* occur sympatrically, although some overlap is possible between *Omalisus fontisbellaquaei* and *O. sanguineus* in Croatia and Bosnia Herzegovina and between *O. fontisbellaquaei* and *O. sanguinipennis* in North Eastern Italy. The ranges of two species of *Thilmanus* in the West Mediterranean islands and Southern France also do not overlap. The high level of endemism in Omalidae can be ascribed to the very low vagility of females due to their incomplete metamorphosis and resulting flightlessness.

Constitution of Omalidae and relationships with elateroid families: The long accepted close relationship between Omalidae and Lycidae have low support from adult morphology and recently were strongly questioned by molecular data (Bocakova *et al.* 2007), which placed Omalidae together with Drilidae and Elateridae. Both Omalidae and Drilidae share a very similar type of male genitalia, the shape of pronotum, antennae and cranium. The detailed comparison of these families is difficult when female morphology is affected by neoteny in different degrees and the larvae and females of most groups are unknown.

The contents of Omalidae was changed when *Pseudeuano* Pic, 1901 was transferred to Drilidae and *Thilmanus* to Lycidae (Crowson 1972, Kazantsev 2005). Crowson (1972) excluded *Pseudeuano* from Omalidae on the basis of the absence of prosternal process, the structure of the elytra and the absence of epipleura. Although the prosternal process is absent in both *Pseudeuano* and the closely related *Euano*, unlike *Drilus* Olivier, 1790 both of these genera have a much longer prosternum resembling those of *Omalisus*. Further characters used for separation of Drilidae and Omalidae, such as the structure of the elytra was shown to be highly variable in related groups. Therefore, the position of these genera should be based on the multiple character cladistic analysis. Unfortunately, further morphological data is not available as we know only larvae and females of *Drilus* and *Selasia* in Drilidae and *Omalisus* in Omalidae. Additionally, the females of these groups differ in the levels of the ontogenetic modifications: the females of *Drilus* are almost com-

pletely larviform and those of *Omalisus* have a partly metamorphosed thorax with vestigial elytra and therefore the comparison of homological structures is impossible. The females or larvae of other genera of both families are unknown. For this reason, we are not able to build the phylogenetic hypothesis on the parsimony analysis and we leave their position as proposed by Crowson (1972).

Phaeopterus was until now considered to be a subgenus of *Omalisus* and both genera are very close to each other in external morphology and their close relationships has not been questioned. Due to the shape of the male genitalia which resemble those of *Thilmanus* we propose the genus status for *Phaeopterus*.

The relationship of *Thilmanus* was a subject of a long lasting controversy after Crowson (1972) tentatively transferred this genus to Lycidae. Later, the genus was returned to Omalidae by Bocak & Bocakova (1990), classified in Drilidae by Medvedev and Kazantsev (1992), and re-transferred to Lycidae by Kazantsev (2005). The main problem of the *Thilmanus* classification is the fact that we must base all conclusions solely on male morphology and additionally there are disagreements among authors even in the interpretation of the morphological characters. Crowson (1972) based his opinion on the long lycid-like trochanters of *Thilmanus*, the shape of the prosternal process, the absent elytral epipleura, and absence of the rows on the elytra. Crowson (1972) mentioned a well developed tentorium, which Kazantsev (2005) found to be reduced. Similarly, Crowson reported an absent epipleura while Kazantsev reported a well developed epipleura. Finally Crowson noted an absent reticulation on the elytra and Kazantsev reported reticulation on the elytra.

Kazantsev (2005) based the placement of *Thilmanus* in Lycidae and the definition of the subfamily Thilmaninae on the following characters:

a) Wing venation and the presence of the anal lobe. The anal lobe is known only in *Thilmanus* and therefore does not support its placement in Lycidae. Modification of the hind wings is common in tiny, soft-bodied and rarely flying insects. The considerable modification of the hind wing is known for example in the lycid genus *Alyculus* Kazantsev, 2000 (Kazantsev 2005), although the wing venation is generally uniform in lycids (Bocak & Bocakova 1990).

b) Seven ventrites in the male abdomen. All Lycidae have eight male abdominal ventrites unlike the seven ventrites in *Thilmanus*. Kazantsev (2005) considered the number of ventrites to be an autapomorphy of Thilmaninae in Lycidae. All genera of Omalidae as understood here, *Omalisus*, *Phaeopterus* and *Thilmanus*, have seven ventrites. Therefore, it cannot be rejected that seven visible ventrites were present in the ancestor of Omalidae, including *Thilmanus*.

c) Tibial spurs present in male legs of *Thilmanus*. Tibial spurs are known and were illustrated by Kazantsev (2005) in numerous groups of Lycidae, in Phengodidae and Cantharidae. We found tibial spurs similar to those of *Thilmanus* in *Omalisus* and *Phaeopterus*. Concerning the distribution of the character states presented in all Elateroid families this character cannot be used for definition of the subfamily Thilmaninae and it does not support classification of *Thilmanus* in Lycidae.

d) Tentorium reduced to non-connected ventral arms in *Thilmanus* (Kazantsev 2005: 94) or tentorium absent (Kazantsev 2005: 218). All lycids have considerably reduced or absent tentorium similar to almost all families classified previously in Cantharoidea. This character seems to be correlated with soft-bodiedness, as the group of cantharoid families was found to be polyphyletic by Bocakova *et al.* (2007).

e) Different structure of the prosternum and the corresponding part of the mesosternum. The structure of prosternum in *Omalisus* is similar to Elateridae and accepting the recent findings of the relationships between Omalidae and Elateridae (Bocakova *et al.* 2007) the reduction of the prosternal process can be affected by soft-bodiedness and the very tiny body of *Thilmanus*. The length of the prosternum is variable in Lycidae, Drilidae and Omalidae. Although the prosternal process is present only in *Omalisus* and *Phaeopterus*, the prosternum in *Thilmanus*, *Euanoma* and *Pseudeuanoma* is much longer than in Lycidae or *Drilus* (Bocak & Bocakova 1990, Kundrata & Bocak 2007). Considering the variability in the shape of the prosternum in all these groups, the form found in *Thilmanus* does not indicate a relationship with Lycidae.

f) Reticulate cells present in the elytra. The elytra of *Thilmanus* are irregularly sculptured and it is hard to describe them as reticulate. Additionally, the clearly reticulate elytra are known in *Omalisus*

and therefore even if we accept the state of this character in *Thilmanus* as reticulated this character state does not support unambiguously the placement of *Thilmanus* in Lycidae. The elytral reticulation known in *Phaeopterus* represents an intermediate state between *Omalisus* and *Thilmanus* and we can see the apparent tendency for reduction of the strength of the elytral costa 6 in *Phaeopterus* and consequently the shortening of the pleural region, with both the prominent costa 6 absent and epipleuron shortened in *Thilmanus*. The vestigial elytra of female *Omalisus* have irregular punctures in elytra although the males have the punctures in the regular rows. Additionally, we have found some extremely small specimens of *Platycis minutus* (Fabricius, 1787) (Lycidae) with a reduced number of longitudinal costae and a decreased number of elytral cells. Specimens with reduced and fully developed number of elytral costae belonged to a single population and the degree of reduction was correlated with the body size.

All these findings support the hypothesized process of reduction of elytral costae and regular rows of punctures in extremely small or soft-bodied elateroid beetles.

g) Non-coadapted abdomen in *Thilmanus*. The non-coadapted margins of the elytra and the abdomen are a rule in soft-bodied beetle families and have developed multiple times in various groups (e.g. *Malachius* in Cleroidea: Melyridae and most cantharoid families in Elateroidea including Lycidae). The possibility of independent origin of non-coadapted abdomen in Omalidae cannot be excluded considering the evolution of this character in other soft-bodied families.

Although Kazantsev (2005) tried to solve the position of *Thilmanus*, he did not study or include *Omalisus* and *Phaeopterus* in his analysis. Additionally, he was misled by the already refuted idea that neoteny is the ancestral state in Coleoptera and that Lycidae are the most basal group of Polyphaga which is the sister group of Neoptera (Kazantsev 2005, 2006, see also Beutel *et al.* 2007). Unfortunately, Kazantsev (2005) did not discuss in detail at least the most important characters and he completely omitted such characters as male genitalia. The male genitalia are very similar to those of *Phaeopterus* (Omalidae) and they differ from all known types of male genitalia in Lycidae (Bocak & Bocakova 1990). Similarly, we can see different shapes of the cranium, antennae

(Fig. 20), structure of the elytra, and tarsi in *Thilmanus* and Lycidae.

To sum up, we propose to classify *Thilmanus* in Omalidae on the basis of the male genitalia which are very similar to those of *Phaeopterus* (Figs 34–38), and which represent the type unknown in Lycidae. The classification of *Phaeopterus* in Omalidae has not yet been seriously questioned by any student of cantharoid beetles and some traits in the morphology of *Phaeopterus* exhibits intermediate characters states between *Omalisus* and *Thilmanus* in several aspects. When we compare *Thilmanus* with *Phaeopterus* we can find a very similar shape of the antennomere 3, very narrow basal part of antennomeres 5–10, a similar shape of the male genitalia, and a similar shape of the head. The genera *Phaeopterus* and *Thilmanus* differ in the presence/absence of rows of punctures forming the elytral costae and lack of lateral longitudinal keels in the pronotum although some inconspicuous keels are traceable in some specimens of *Thilmanus*. *Omalisus* and *Phaeopterus* share similar lateral keels in the pronotum, well-developed reticulation of the elytra and they are very similar in general appearance. As we have found several new characters which connect *Thilmanus* and *Phaeopterus* and which was until now classified as a subgenus of *Omalisus*, we propose to keep *Thilmanus* in Omalidae.

The character states supporting Kazantsev’s hypothesis are known in other soft-bodied families of Elateroidea and these characters misled coleopterologists for a long time. Geisthardt (1979) showed that there is more correspondence between muscles of neoteny affected females of Lampyridae and neuropteroid larvae than between the lampyrids and remaining beetles. Recently, Lawrence (1988) lumped Cantharoidea with Elateroidea into a single superfamily when he recognized the low reliability of character modifications connected with soft-bodiedness. The polyphyly of the earlier hypothesized cantharoid clade was clearly demonstrated by Bocakova *et al.* (2007). The diagnostic characters given for the subfamily Thilmaninae by Kazantsev (2005) when he classified *Thilmanus* to Lycidae do not sufficiently define this subfamily in Omalidae as we are not able to classify *Phaeopterus*, which combines characters of both *Omalisus* and *Thilmanus*.

Nevertheless, the definitive placement of *Thilmanus* deserves further study. Already Crowson (1972) mentioned that the principal problem with

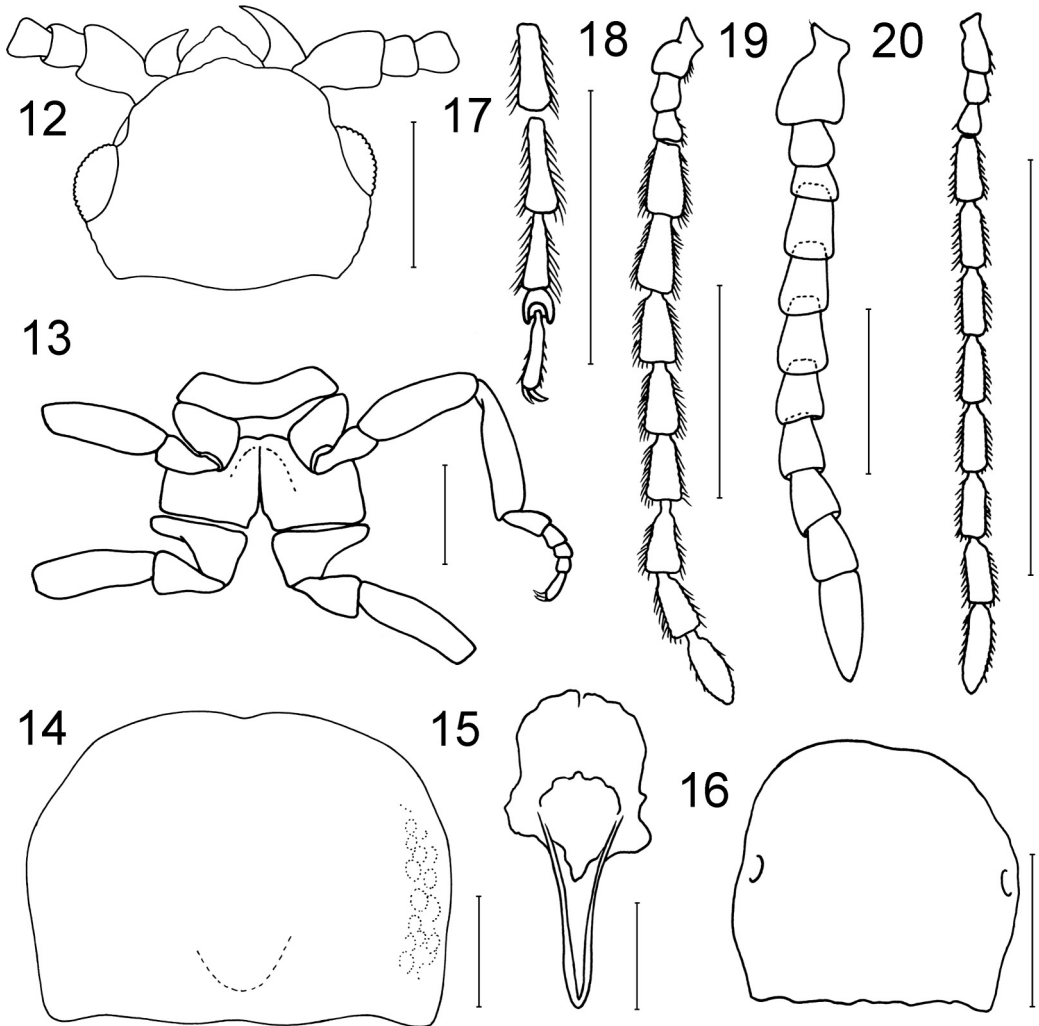
classifying *Thilmanus* was the fact that we know neither immature stages nor females and therefore he postponed description of a family rank taxon for *Thilmanus* in Lycidae and considered his acts as tentative. Further data could be produced when *Thilmanus* is available for DNA study. Unfortunately, most *Thilmanus* specimens known in collections were collected before 1900 and they are not useful for the DNA studies. For further study more extensive material, including immature stages or recently collected specimens appropriately fixed for DNA study are necessary.

We propose here to classify three genera in Omalidae: *Omalisus* (5 species), *Phaeopterus* (1 species) and *Thilmanus* (2 species). The position of *Euanoma* and *Pseudeuanoma* in Drilidae follows Crowson (1972) although some characters such as the morphology of male genitalia and the long prosternum resemble Omalidae and relationships of these genera should be studied in the future.

Key to genera and species of the family Omalidae

1. Elytra with ten rows of regular rounded punctures which form nine longitudinal costae in elytra, pronotum with keel attached to posterior margin and parallel with lateral margins of pronotum..... 2
 - Elytra irregularly sculptured, pronotum at most with inconspicuously elevated area along lateral margins, without any sharp keel 7
 - Thilmanus* Gemminger 7
2. Parameres with externally curved apices (Figs 28–32), pronotal keels inconspicuous to absent frontally, elytral costa 6 strongly elevated usually in whole length or at least in basal two thirds of elytral length (Fig. 1), antennomere 4 about 1.3 times longer than combined length of antennomeres 2 and 3 (Figs 1, 19) 3
 - Parameres with simple apices, membranous apically (Figs 34–35), lateral pronotal keels very sharp in whole length, reaching frontal margin of pronotum, costa 6 apparently elevated in basal half of elytral length, antennomere 4 about as long as combined length of antennomeres 2 and 3 (Fig. 18).. *Phaeopterus unicolor* Costa 3
 - *Omalisus fontisbellaquaei* Geoffroy
 - Elytra evenly coloured reddish brown. The Alps Maritimes, Italy, Croatia and Bosnia Herzegovina 4
3. Elytra dark along elytral suture, light brown laterally or whole elytra dark brown to black. Central and Western Europe, eastern part of the Balkan Peninsula, Western Turkey 4
 - *Omalisus fontisbellaquaei* Geoffroy
 - Elytra evenly coloured reddish brown. The Alps Maritimes, Italy, Croatia and Bosnia Herzegovina 4
4. Middle part of pronotal disc shiny 5
 - Middle part of pronotal disc sculptured, at

- most some small slightly shiny patches in the middle of the disc 6
5. Pronotum dark brown to black, phallus very wide at base (Fig. 29). North Eastern Italy (Udine, Castel Nuovo), Croatia, Bosnia Herzegovina *O. sanguinipennis* Castelnau
- Pronotum similarly coloured as elytra to slightly infusate, phallus narrower at base (Fig. 30). France (the Alps Maritimes and Provençal), North Western Italy (Mt. Rossa) .*O. victoris* Mulsant
6. Pronotum dark brown to black, body small (5.0–6.3 mm), phallus as in Fig. 32. South Eastern France (Nice, Menton) *O. nicaeensis* Lesne
- Pronotum brown, only slightly darker than elytra, seldom dark brown, then at least posterior and base of lateral margins brown, body medium sized (7.2–8.3 mm), phallus as in Fig. 31. Italy (Piedmont, Sicily) *O. taurinensis* Baudi
7. Internal margin of paramerae with transverse groove (Fig. 38)..... *T. laticeps* Pic
- Internal margin of paramerae simple (Figs 36, 37)..... *T. obscurus* Baudi



Figs 12–20. *Omalius fontisbellaquaei*, female. 12. Head, dorsally; 13. Pterothorax, ventrally; 14. Pronotum; 15. Terminal abdominal sternite; 16. Terminal abdominal tergite. *Phaeopterus unicolor*, male. 17. Hind tarsus. Antennae. 18. *Phaeopterus unicolor*; 19. *Omalius fontisbellaquaei*, female; 20. *Thilmanus obscurus*. Scales = 0.5 mm.

Genus *Omalisus* Geoffroy, 1762

(Figs 1–16, 19, 21–26, 28–32)

Omalisus Geoffroy, 1762: 179.

Homalilus Illiger, 1801: 139 (unjustified emendation).

Omalysus Hope, 1831: 26 (incorrect subsequent spelling).

Type species. – *Omalisus fontisbellaquaei* Geoffroy, 1762 (by monotypy).

Remark. – The type genus, *Omalisus* Geoffroy, 1762, has been conserved by the ICZN (1994).

Differential diagnosis. – *Omalisus* shares with *Phaeopterus* the elevated and stronger elytral costa 6 and the presence of the keels at lateral margins of the pronotum (Fig. 1). These genera differ in the shape of male genitalia (Figs 28–35) with only *Omalisus* having externally curved apices of parameres.

Redescription. – Male. Body small to medium sized, 5.0–8.5 mm (n=87), slightly dorso-ventrally flattened, elytra parallel-sided (Fig. 1), body, well sclerotized, dark brown to black in all species, only elytra brightly red coloured in most species. Head small, including eyes narrower than frontal margin of pronotum, with strong antennal tubercles separated frontally by groove. Surface of cranium roughly sculptured, sometimes with shiny part in vertex. Eye smaller than interocular distance, hemispherically prominent (Fig. 2). Antennae *filiform*, antennomere 1 pear-shaped, antennomeres 2 and 3 short, subequal in length, antennomere 4 longer than combined length of antennomeres 2 and 3, antennomeres 4–10 subequal in length, antennomere 11 longer. Clypeus slightly concave, labrum small, rounded at apex, membranous apically (Fig. 8), mandibles long, robust, curved (Fig. 9). Maxillary palpi with very small palpomere 1, apical palpomere longest, obliquely cut at apex (Fig. 5). Labial palpi tiny, apical palpomere slightly pointed (Fig. 3). Pronotum flat, wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided, posterior angles projected obliquely backwards (Fig. 4), disc roughly sculptured at lateral and frontal margins, shiny in middle part, sculptured and shiny area separated by sharp keel attached to posterior margin, keel gradually weaker to absent frontally (Fig. 4). Prosternum at frontal margin 2.6 times wider than long in shortest part, with short slender prosternal process (Fig. 7). Elytra parallel-sided, with ten rows of round punctures which form nine

continuous costae, flat between elytral suture and strongly elevated costa 6, with outer part forming apparent pleura. Legs slender, slightly compressed, with five tarsomeres (Fig. 6). Male genitalia as in Figs 28–32. Female. Body soft-bodied; mouthparts adult like; antennae and legs shortened, but with same number of antennomeres as male (Fig. 19); elytra and hind wings vestigial (Fig. 24); meso- and metathorax morphologically similar; abdomen physogastrous (Fig. 11).

Distribution. – The distribution of *Omalisus* almost corresponds with the range of the whole family and covers Western and Central Europe from the Atlantic coast to North Eastern Poland and in the Mediterranean from Southern France, to Italy, the Balkan Peninsula, and Western Turkey. *Omalisus* does not occur in the Mediterranean islands (Sardinia, Corsica) from where only the genera *Phaeopterus* and *Thilmanus* are recorded.

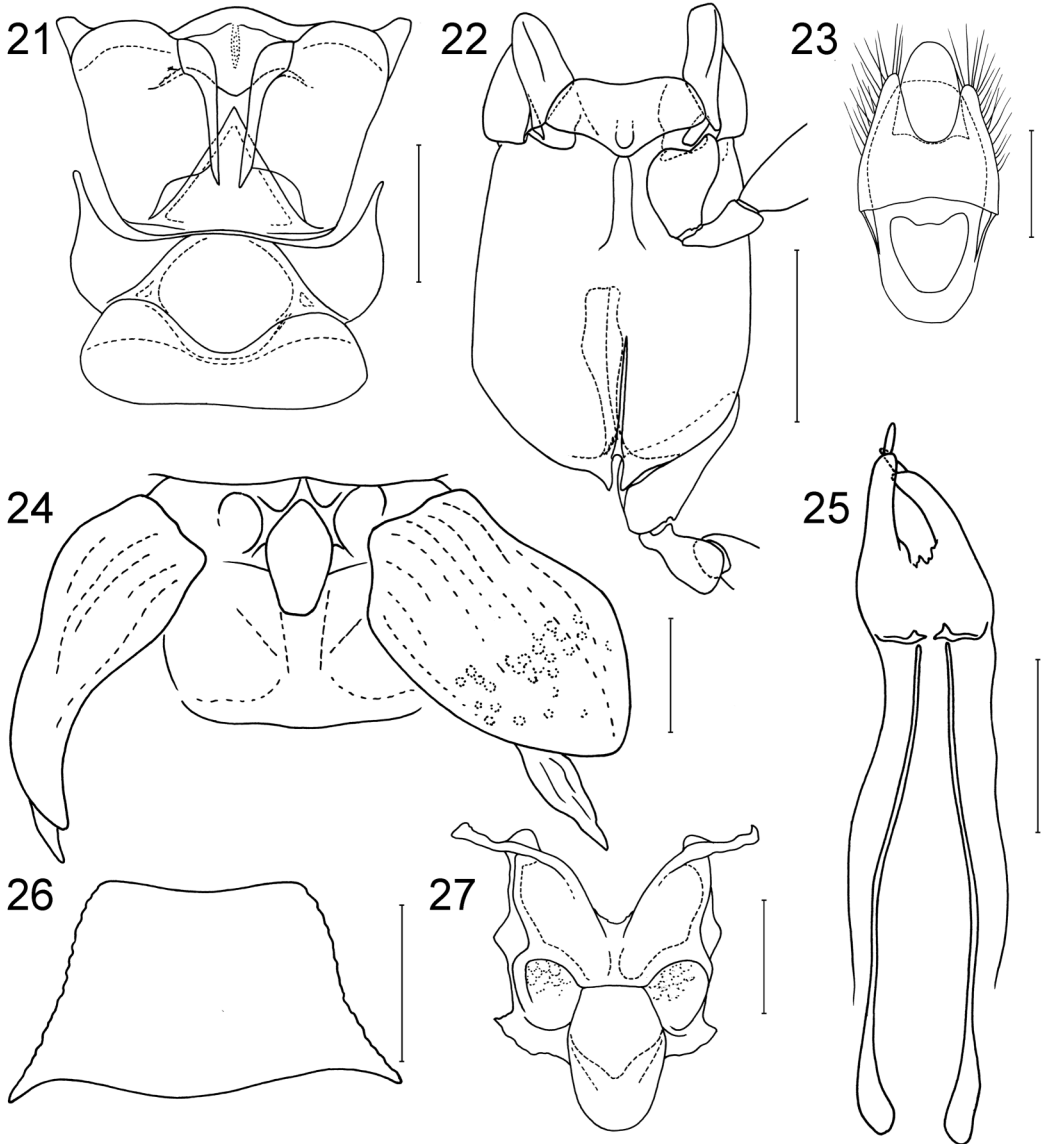
Taxonomic discussion. – Five species are placed in *Omalisus* and only one of them, *O. fontisbellaquaei*, is widespread and easily recognizable by its dark brown to black colouration of elytra. Additionally four *Omalisus* species with red elytra and a dark brown body are known in Southern Europe from the southern coast of France, through Italy to Dalmatia, Montenegro, and Bosnia Herzegovina. *Omalisus nicaeensis* is the easily recognizable species which differs from the remaining ones by its morphology and occurrence in late autumn and early winter. The further three species *O. victoris*, *O. taurinensis*, and *O. sanguinipennis* are very closely related to each other and differ slightly in a few characters (structure of the pronotal disc, coloration of the pronotum, and the shape of the phallus). These species have vicariant ranges and traditionally were considered full species although it would be possible to lower their status to the subspecies level considering the low morphological differentiation, which suggests their common origin and the isolation of these species during recent glacial maxima. We leave their species status as they can be recognized and there is not available any proof that they hybridize. The lack of a hybrid zone may be caused by the extremely low vagility of females, but our knowledge can be incomplete considering the extreme rarity of these taxa. Further research should be based on the molecular phylogeny of the group if properly fixed material is available.

***Omalisus fontisbellaquaei* Geoffroy, 1785**

(Figs 1–16, 19, 21–26, 28)

Omalisus fontisbellaquaei Geoffroy, 1785: 64.*Omalisus nigricans* Schilsky, 1888: 188.*Omalisus rougeti* J. E. Olivier, 1884: 42 (*Phosphaenus*).*Omalisus suturalis* G. A. Olivier, 1790: 4.

Differential diagnosis. – *O. fontisbellaquaei* can be easily recognized by the coloration and the body size. It is the only *Omalisus* with a dark strip along the elytral suture or with whole elytra concolorous dark.



Figs 21–27. *Omalisus fontisbellaquaei*. 21. Pterothorax, dorsally, male; 22. Pterothorax, ventrally, male; 23. Terminal abdominal sternites, male; 24. Pterothorax, dorsally, female; 25. Ovipositor; 26. Mesoscutum. *Thilmanus obscurus*. 27. Pronotum. Scale = 0.5 mm (Figs 22, 24, 25), scale = 0.25 (Figs 21, 23, 26, 27).

Redescription. – Male. Body medium sized, 5.2–7.0 mm (n=39), slightly dorso-ventrally flattened, parallel-sided (Fig. 1); dark brown to black, only elytra with lateral margins and apex light brown. Head small, including eyes slightly narrower than frontal margin of pronotum, with strong antennal tubercles separated by deep groove frontally. Surface of cranium in most parts densely roughly sculptured, finely sculptured behind antennal tubercles. Eye small, interocular distance 1.38 times maximum eye diameter in lateral view, hemispherically prominent. Antennae *filiform*, gradually slenderer to apex, antennomere 1 pear-shaped, robust, antennomeres 2 and 3 short, subequal in length, shiny, finely sculptured, antennomere 4 1.2 times of the combined length of antennomeres 2 and 3, antennomeres 4–10 subequal, antennomere 11 1.5 times length of antennomere 10, antennomeres 4–11 densely sculptured, matt. Clypeus slightly concave, labrum small, rounded at apex, mandibles long, robust, curved (Fig. 9). Maxillary palpi with very small palpomere 1, palpomeres 2 and 3 triangular, apical palpomere robust, parallel-sided, obliquely cut at apex (Fig. 5). Labial palpi tiny, apical palpomere slightly pointed (Fig. 3). Pronotum flat, 1.6 times wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided, posterior angles projected obliquely backwards (Fig. 4), disc roughly sculptured at lateral and frontal margins, shiny in middle part, sculptured and shiny area separated by sharp keel attached to posterior margin, keel gradually weaker to absent frontally (Fig. 4). Elytra parallel-sided, with ten rows of round punctures which form continuous costae, flat between elytral suture and strongly elevated costa 6, with outer part forming apparent pleura. Elytral costae shiny, with scarce erected pubescence. Legs slender, slightly compressed, densely pubescent (Fig. 6). Male genitalia with the wide basal part of the phallus which narrows gradually to apex (Fig. 28). Female. – See the description of the genus (Fig. 11).

Material examined. – AUSTRIA: Carinthia, Sachsenburg, 1 male (NHMP); Voralberg, Feldkirch, 1 male, Dr Feige leg. (NHMP); Nieder Österreich, Voralpen, 1 male, Mandl leg. (NHMP). BULGARIA: Sliven, Rakovo, vi. 1984, 1 male, Kadlec & Vorisek leg. (LMBC); Vel. Trnovo, 30. v. 09, 1 male, Rambousek leg. (NHMP); Rodopi, Dobrostan, vi. 64, 1 male, J. Jelinek leg. (NHMP); Stribnec, vi. 1981, 1 male, J. Strejcek leg. (LMBC). CROATIA: Cerkenica, 1 male, Dr. J. Fleischer leg. (NHMP); Obir., vii. 1935, 3 males, Vsetecka

leg. (MHNP, LMBC); Plitvice, 7. vii. 1910, 1 male, Hochetlinger leg., (RCSL); Istria, Sistiana, 1 male, Th. Wanka leg. (NHMP). CZECH REPUBLIC: Karov, 9. vi. 1907, 1 male (NHMP); Moravia, Radhost, 1 male, J. Fleischer leg. (NHMP); Moravia, Brno, 1 male, J. Fleischer leg. (NHMP); Bohemia, Davle, 11. vi. 1 male, Zeman leg. (NHMP); Skryje, 1 male, Vsetecka leg. (LMBC); Srbsko, v. 1939, 1 male, Vsetecka leg. (LMBC); Central Bohemia, Lovos, vi. 1976, 2 males, J. Davidova leg. (LMBC); Nove Straseci, vi. 1976, 1 male, K. Rebl leg. (LMBC); Central Bohemia, Oupon, vii. 1973, 1 male, Z. Strejcek leg. (LMBC). FRANCE: Savin. Alp., 1907, 1 male, Rambousek leg. (NHMP); Dreux, 1 male, J. Achard leg. (NHMP). GERMANY: Wurttemberg, Ulm, 6. 1897, 1 male (NHMP); S. W. Bayern, Günzburg a. D., 1 male (NHMP); Bonn, 1 female, 1890, Bertkau leg. (DEIC). HUNGARY: Sopron, 1 male, Moczarski leg. (NHMP); Harkany, v. 1976, 2 males, V. Svihla leg. (NHMP, LMBC). POLAND: Zakopane, Tatra, 1 male, Sterba leg. (NHMP). ROMANIA: Carp. mont., Balzatul, 1932, 1 male, Vsetecka leg. (LMBC). SLOVAKIA: Remetske Hamre, vii. 1973, 1 male, V. Svihla leg. (LMBC); Cierny Vah, vi. 1937, 1 male, Vsetecka leg. (LMBC); Remetske Hamre, vii. 1970, 1 male, Zirovnický leg. (LMBC); Harmanec, vii. 1987, 1 male, L. Bocak leg. (LMBC); Muran, vi. 1971, 1 male, Zirovnický leg. (LMBC); Slovakia, Nova Sedlica, vii. 1967, 1 male, Zirovnický leg. (LMBC); Eastern Karp., Rabiska skala, vii. 1973, 1 male, J. Strejcek leg. (LMBC); Eastern Karp., Nova Sedlica, vii. 1973, 1 male, J. Strejcek leg. (LMBC). TURKEY: Abant Daglari, Boludag Gecidi, 720 m, vi. 1986, 1 male, S. Kadlec leg. (LMBC); Prov. Kuklarelí, Demirkoy, vi. 1989, 1 male, Barries & Cate leg. (LMBC). UKRAINE: Kuzy, 1 male, (NHMP). YUGOSLAVIA: Strpec, vii. 1985, 1 male, M. & J. Hladil leg. (LMBC).

Measurements. – BL 5.7 mm, WH 1.57 mm, PL 0.79 mm, PW 1.27 mm, Ediam 0.34 mm, Edist 0.47 mm.

Type locality. – Fontainebleau (France).

Distribution. – *O. fontisbellaquaei* is the only widespread and the most common species of the family. It is found in Western and Central Europe north of the Alps and in the Balkan (from the Netherlands and Belgium to North Eastern Poland, further from South-eastern Europe to Hungary, Romania, Bosnia and Herzegovina, Croatia, Bulgaria, and Western Turkey). *O. fontisbellaquaei* occurs very locally but it is not rare in some places and sometimes can be collected in large quantities.

Biology. – *O. fontisbellaquaei* lives in various habitats from xerothermous shrubs or oak forests to montane fir and beech forests. The biology of the larva was thoroughly described by Burakowski (1988). Adult males are capable of flight, but they

usually sit motionless on leaves in the lowest forest stratum. Females have vestigial elytra and hind wings (Bertkau 1891, Geisthardt, 1974), remain in the surface soil layers and only a few specimens have been collected (Burakowski 1988).

***Omalisus nicaensis* Lesne, 1921**

(Fig. 32)

Omalisus nicaensis Lesne, 1921: 181.

Differential diagnosis. – The pronotum is characteristically dark coloured with a punctuated middle of the disc and this species has the smallest body in the genus. Male genitalia are characterized by a gradually widened phallus at the base (Fig. 32).

Redescription. – Male. Body small, 5.0–6.6 mm (n=8), slightly dorso-ventrally flattened, parallel-sided, dark brown to black, only elytra light reddish brown. Head small, including eyes only slightly narrower than frontal margin of pronotum, with conspicuous antennal tubercles separated frontally by wide, shallow groove. Surface of cranium densely, roughly sculptured. Eye small, interocular distance 1.41 times maximum eye diameter in lateral view, hemispherically prominent. Antennae *filiform*, very slender, antennomere 1 pear-shaped, robust, antennomeres 2 and 3 short, subequal in length, shiny, finely sculptured, antennomere 3 1.4 times of the combined length of antennomeres 2 and 3, antennomeres 4–10 subequal, antennomere 11 1.23 times length of antennomere 10, all antennomeres densely sculptured, matt. Clypeus slightly concave, labrum small, rounded at apex, mandibles long, robust, curved. Maxillary palpi slender, with very small palpomere 1, palpomeres 2 and 3 almost parallel-sided, only slightly widened to apex, apical palpomere slender, parallel-sided, obliquely cut at apex. Labial palpi tiny, slender, apical palpomere slightly pointed. Pronotum flat, 1.3 times wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided, posterior angles projected obliquely backwards, whole disc roughly sculptured, only slightly shiny in middle part, sharp keel parallel with lateral margins present in most of pronotal length, keel absent frontally. Elytra parallel-sided, with ten rows of round punctures which form continuous costae, flat between elytral suture and strongly elevated costa 6 in almost whole elytral length, outer part of elytra forms basally apparent pleura.

Elytral costae shiny, with scarce erected pubescence. Legs slender, slightly compressed, densely pubescent. Male genitalia as in Fig. 32. Female. Unknown.

Measurements. – BL 5.25 mm, WH 1.32 mm, PL 0.78 mm, PW 0.99 mm, Ediam 0.33 mm, Edist 0.37 mm.

Type locality. – Nice, Canal de la Vésubie, Menton (France).

Distribution. – *O. nicaensis* is known from the series of specimens collected mostly by French entomologists in Nice and Menton in the 1920's and a single specimen collected in Nice in 1849. No specimen was collected anywhere else and we do not know any recent record of this species. Considering the present urbanization of the area where the species was collected, it is possible that the original habitats have been destroyed and the species is extinct.

Biology. – *O. nicaensis* is the only species in the genus with adults active in late autumn and winter (November to January according to local data from the studied specimens). All remaining omalid species were collected in adult stage from May to July depending on the latitude and altitude of the habitat. The shift in the occurrence of adults may play a role in the reproductive isolation of this species.

Material examined. – FRANCE: Nice, Canal de la Vésubie, 1 male, A. Buchet leg. (MHNP); Menton, Alpes Maritimes, xii. 1920, 1 male, L. Turinetti leg. (MHNP, identified by P. Lesne); Nice, xi. 1849, 1 male, Bauer leg. (MHNP); Menton, Alpes Maritimes, xii 1921, i.1921, 3 males, L. Turinetti leg. (MHNP); Nice, Canal de la Vésubie, 1 male, St. Cl. Deville leg. (NHMW); Riviera, Menton, 6. xii. 1920, 1 male, Dr. Rambousek leg. (NHMP).

Remark. – We were not able to locate the type of *O. nicaensis*, but the identity of the species is confirmed by the study of the specimen identified by P. Lesne.

***Omalisus sanguinipennis* Laporte, 1840**

(Fig. 29)

Omalisus sanguinipennis Laporte, 1840: 263.

Differential diagnosis. – *O. sanguinipennis* has a very wide base of the phallus and almost parallel-sided apical two thirds of its length (Fig. 29). This shape of phallus has not been found in other

species with red elytra. The pronotum is regularly dark brown to black in *O. sanguinipennis*.

Redescription. – Male. Body medium sized, 5.8–8.5 (n=27), slightly dorso-ventrally flattened, parallel-sided, dark brown, only elytra light reddish brown. Head small, including eyes apparently narrower than frontal margin of pronotum, with conspicuous antennal tubercles separated frontally by wide, rather shallow groove. Surface of cranium in most parts densely, quite roughly sculptured, structure finer behind antennal tubercles. Eye small, interocular distance 1.12 times maximum eye diameter in lateral view, hemispherically prominent. Antennae *filiform*, gradually slenderer to apex, antennomere 1 pear-shaped, robust, antennomeres 2 and 3 short, subequal in length, shiny, finely sculptured, antennomere 4 1.4 times of the combined length of antennomeres 2 and 3, antennomeres 4–10 subequal, antennomere 11 1.3 times length of antennomere 10, all antennomeres densely sculptured, matt. Clypeus slightly concave, labrum small, rounded at apex, mandibles long, robust, curved. Maxillary palpi with very small palpomere 1, palpomeres 2 and 3 triangular, apical palpomere robust, parallel-sided, obliquely cut at apex. Labial palpi tiny, apical palpomere slightly pointed. Pronotum flat, 1.4 times wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided, posterior angles projected obliquely backwards, disc roughly sculptured at lateral and frontal margins, shiny in middle part, sculptured and shiny area separated by sharp keel attached to posterior margin, keel gradually weaker to absent frontally. Elytra parallel-sided, with ten rows of round punctures which form continuous costae, flat between elytral suture and strongly elevated costa 6 in frontal two thirds of elytral length, outer part of elytra forms basally apparent pleura. Elytral costae shiny, with scarce erect pubescence. Legs slender, slightly compressed, densely pubescent. Male genitalia with very wide base of phallus (Fig. 29). Female. Unknown

Measurements. – BL 7.35 mm, WH 1.84 mm, PL 1.07 mm, PW 1.50 mm, Ediam 0.43 mm, Edist 0.48 mm.

Type locality. – Dalmatia (Croatia).

Distribution. – North eastern Italy, Croatia, Montenegro.

Material examined. – CROATIA: Dalmatia, 1 male, coll. Bourgeois (without further data) (MHNP); Dalmatia, 1 male (MHNP); Split distr., Dugopolje, 5 km SE to Sv. Jure Mt., 43.33N, 16.38E, 550 m, 31. v. 2004, 1 male, R. Constantin (RCSL); Dalmatien, Ragusa [=Dubrovnik], 1 male, coll. Reitter (ZMBC); Dalmatia 1 male (ZMBC); Dalmat., 1 male, (NHMP); Dalmatia, Ragusa [=Dubrovnik], 1 male, Dr J. Fleischer leg. (NHMP); Dalmatia, Ragusa [=Dubrovnik], 4 males, Dr. Feige leg. (ZMBC); Meini, 1 male, Dr. J. Fleischer leg. (NHMP); Biokovo Plan, Dalmatia, 1934, 1 male, Dr Jurecek leg. (NHMP); Dalmatia, Makarska, 1 male (NHMP); Dalmatia, Dubrovnik, 1 male, (NHMP); Dalmatia, Biokovo, 1 male, (NHMP); Dalmatia, Hercegovci, iv. 1936, 3 males, A. Matejka leg. (NHMP). MONTENEGRO: Bacici pr. Budva, v. 1975, 2 males, J. Strejcek leg. (LMBC); Sutomoran, Sutomore env., 800 m, v. 1984, 1 male, J. Strejcek leg. (LMBC); Poljice 900 m, 23. 6. 11, 1 male, Spaney - Schumacher S. V. leg. (ZMBC). ITALY: Castelnuovo, 1 male, Hummler leg. (MZMB); P° di Tanamea - 800 m, Udine, Italia, 15. vii. 1966, 1 male, R. Constantin leg. (RCSL); Castelnuovo, 1895, 1 male, Hummler leg. (ZMBC). Coll. Armitage, 1 male, (without further data) (MHNP); v. 1939, 1 male, Koch leg. (without further data) (ZMBC).

Remark. – No type specimen(s) of *O. sanguinipennis* was found in the MHNP despite intensive search. As the identity of this species has not yet been questioned and it is the only species of *Omalisus* with reddish brown elytra occurring in the type locality, we consider the identity to be firmly established.

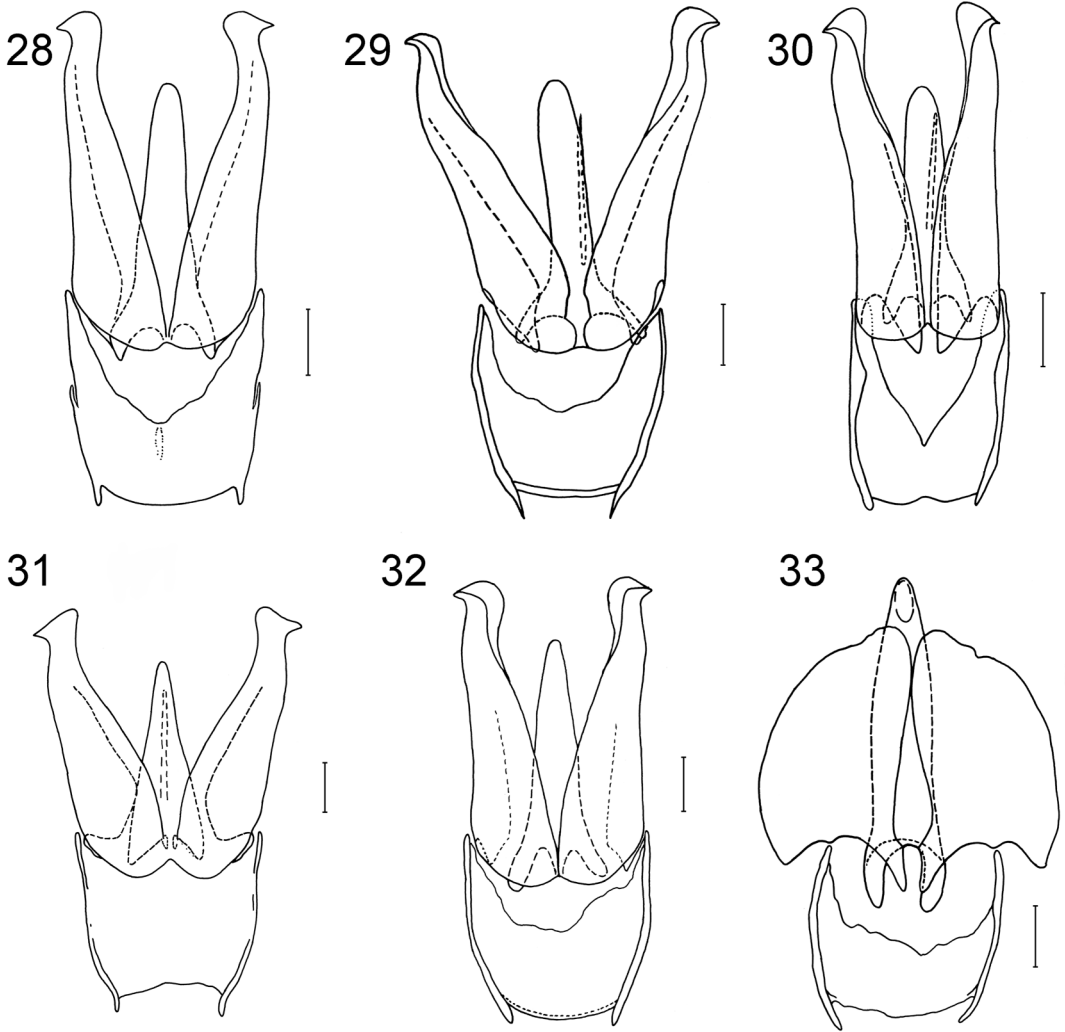
***Omalisus taurinensis* Baudi, 1872**

(Fig. 31)

Omalisus taurinensis Baudi, 1872: 93.

Differential diagnosis. – *O. taurinensis* has the whole pronotal disc densely sculptured. The weak lateral pronotal keels is reminiscent of *O. nicaeensis*, but these species differ in the colouration of the basal three antennomeres which are reddish brown in *O. taurinensis* and in the shape of phallus which is slender and triangular in *O. taurinensis* (Figs 31).

Redescription. – Male. Body small to medium sized, 5.0–8.3 (n=4), slightly dorso-ventrally flattened, parallel-sided, dark brown to black, elytra light reddish brown, pronotum brown, slightly lighter than other brown coloured body parts, antennomeres 1–3 brown, apparently lighter than remaining ones. Head small, including eyes about as wide as frontal margin of pronotum, with conspicuous antennal tubercles separated frontally by wide, very shallow groove. Surface of cranium densely, roughly sculptured, shiny area behind an-



Figs 28–33. Male genitalia, ventrally. 28. *Omalisus fontisbellaquaei*; 29. *O. sanguinipennis*; 30. *O. victoris*; 31. *O. taurinensis*; 32. *O. niceensis*; 33. *Euanoma nigricornis*. Scales = 0.1 mm.

tenal tubercles small to absent. Eye small, interocular distance 1.41 times maximum eye diameter in lateral view, hemispherically prominent. Antennae *filiform*, very slender, antennomere 1 almost parallel-sided, slender, antennomeres 2 and 3 short, subequal in length, shiny, finely sculptured, antennomere 4 1.64 times of the combined length of antennomeres 2 and 3, antennomeres 4–10 subequal, antennomere 11 1.20 times length of antennomere 10, all antennomeres densely sculptured,

mat. Clypeus slightly concave, labrum small, rounded at apex, mandibles long, robust, curved. Maxillary palpi slender, with very small palpomere 1, palpomeres 2 and 3 slightly widened to apex, apical palpomere parallel-sided, obliquely cut at apex. Labial palpi tiny, slender, apical palpomere slightly pointed. Pronotum flat, 1.3 times wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided, posterior angles projected obliquely backwards, whole

disc roughly sculptured, sometimes slightly shiny in middle part, weak slender keel parallel with lateral margins present in most of pronotal length, keel absent frontally. Elytra parallel-sided, with ten rows of round punctures which form continuous costae, flat between elytral suture and strongly elevated costa 6 in almost whole elytral length, outer part of elytra forms basally apparent pleura. Elytral costae shiny, with scarce erected pubescence. Legs slender, slightly compressed, densely pubescent. Male genitalia with phallus triangular, gradually narrowing to apex (Fig. 18). Female. Unknown.

Measurements. – BL 7.8 mm, WH 2.00 mm, PL 1.13 mm, PW 1.45 mm, Ediam 0.41 mm, Edist 0.58 mm.

Type locality. – Piedmont (Italy).

Distribution. – Italy, except the North Eastern region.

Material examined. – ITALY: Turin, 1 male (MHNP); Sicily, 1 male, (without further data) (MHNP); Crissolo, 7. vi. 1906, 1 male, Pinker leg. (NHMW); Turin, 2 males, Ghil. leg. (ZMBC); Susa, 1 male (ZMBC); Piedmont, 1 male, A. Fiori leg. (ZMBC).

Remark. – We did not have an opportunity to study the type of *Omalisus taurinensis*. The type should be deposited in the Natural History Museum in Torino, but the collection is closed and not available for study.

***Omalisus victoris* Mulsant, 1852**

(Fig. 30)

Omalisus victoris Mulsant, 1852: 79.

Differential diagnosis. – The pronotum of *O. victoris* is regularly reddish brown and the disc of pronotum is only seldom slightly infuscate. Disc of pronotum is shiny with very scarce punctuation unlike *O. taurinensis* and *O. nicaeensis* which have the disc of pronotum densely punctuated. The phallus is widest at base and then steeply narrowed (Fig. 30).

Redescription. – Male. Body medium sized, 6.6–7.2 (n=9), slightly dorso-ventrally flattened, parallel-sided, dark brown, elytra light reddish brown, pronotum same colour as elytra or infuscate especially in the middle of disc, never dark brown. Head small, including eyes apparently narrower than frontal margin of pronotum, with con-

spicuous antennal tubercles separated frontally by wide, shallow groove. Surface of cranium in most parts densely, roughly sculptured, structure finer behind antennal tubercles. Eye small, interocular distance 1.14 times maximum eye diameter in lateral view, hemispherically prominent. Antennae *filiform*, gradually slenderer to apex, antennomere 1 pear-shaped, robust, antennomeres 2 and 3 short, subequal in length, antennomere 4 1.1 times of the combined length of antennomeres 2 and 3, antennomeres 4–10 subequal, antennomere 11 1.4 times length of antennomere 10, all antennomeres densely sculptured, matt. Clypeus slightly concave, labrum small, rounded at apex, mandibles long, robust, curved. Maxillary palpi with very small palpomere 1, palpomeres 2 and 3 triangular, apical palpomere robust, slightly narrower at base, obliquely cut at apex. Labial palpi tiny, apical palpomere slightly pointed. Pronotum flat, 1.5 times wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided, posterior angles projected obliquely backwards, disc roughly sculptured at lateral and frontal margins, shiny in middle part, glabrous or with light structure in shiny part, sculptured and shiny areas separated by sharp robust keel attached to posterior margin, keel very robust in middle of pronotal length, weaker frontally. Elytra parallel-sided, with ten rows of round punctures which form continuous costae, flat between elytral suture and strongly elevated costa 6 in almost whole elytral length, outer part of elytra forms apparent pleura. Elytral costae shiny, with scarce erected pubescence. Legs slender, slightly compressed, densely pubescent. Male genitalia slender, with parallel-sided paramerae and with moderately basal part of phallus (Fig. 30). Female. Unknown

Measurements. – L 7.4 mm, WH 1.98 mm, PL 1.12 mm, PW 1.68 mm, Ediam 0.46 mm, Edist 0.64 mm.

Type locality. – France.

Distribution. – *O. victoris* is known only from the Alps Maritimes and Provence in France and from the Mt. Rosa in Northwestern Italy.

Biology. – The recently collected specimens were swept from vegetation in shrub habitats.

Material examined. – FRANCE: St. Martin-Vesubie, 1 male, Dr. Martin leg. (without further data) (MHNP); Tenda, Alpi Marittime, vi. 1932, 1 male, A. Dodero leg.

(MHNP); 1 male, Coll. Chevrolat (without further data) (MHNP); Failiffen, 1 male, Desbroch leg. (without further data) (MHNP); Alpes Maritimes, Saint-Martin-Vésubie, 950 m, 10. vi. 1972, 2 males, G. Tempère leg. (RCSL); Alpes de Hts Provence, Colmars, alt. 1800 m, Col de Champs, Battage, 28. vii. 1996, 1 male, R. Constantin (RCSL); Alpes-Maritimes, Col. St Martin, 22. vii. 1956, 1 male, G. Tempère leg. (RCSL). ITALY: Mt Rosa, Macugnaga, Borce, 20. vii. 1 male (NHMB).

Remark. – We were not able to obtain any type material deposited in the Mulsant's collection in Lyon. The concept of this species was stable since its description (Bourgeois 1882, Kleine 1942) and it is followed here.

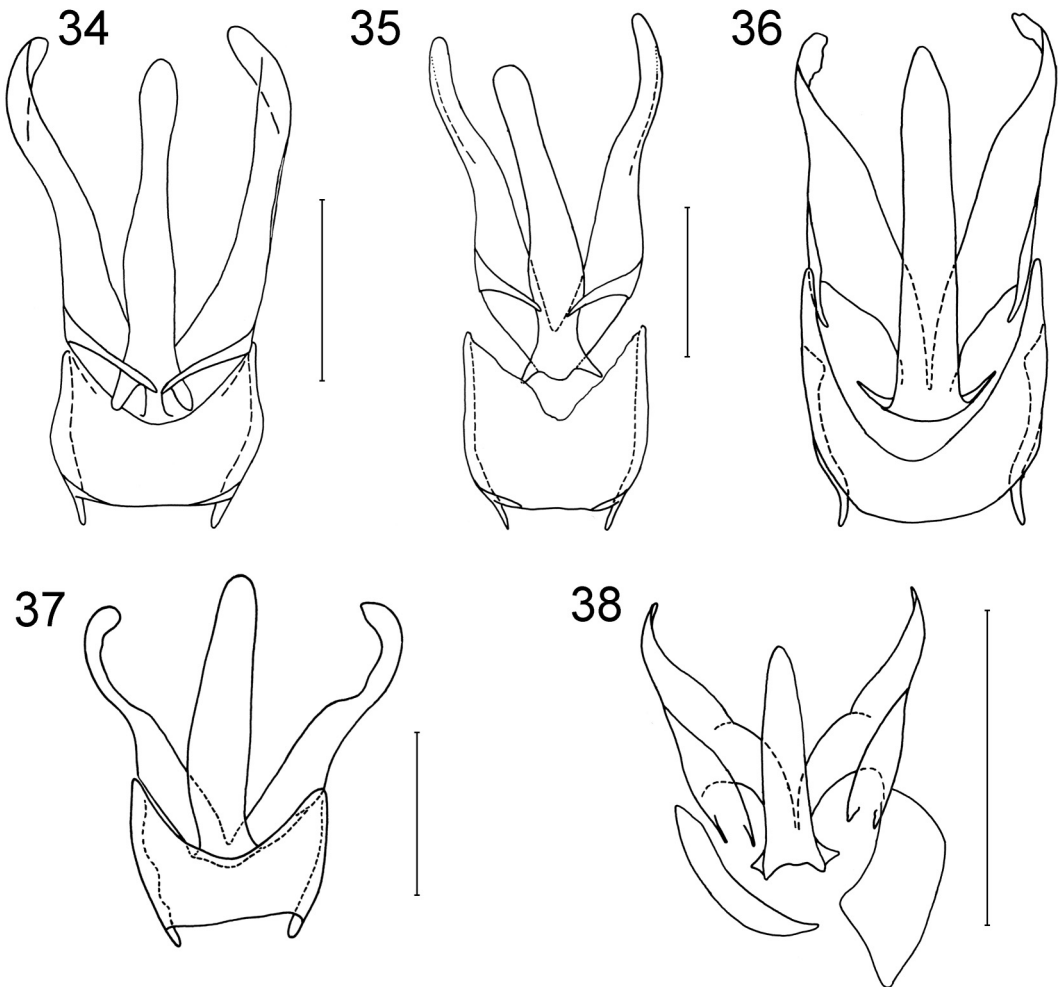
Genus *Phaeopterus* Costa, 1857, stat. n.

(Figs 18, 34–35)

Phaeopterus Costa, 1857: 220.

Type species. – *Phaeopterus unicolor* Costa, 1857 (by monotypy).

Differential diagnosis. – *Phaeopterus* was treated for a long time as a subgenus of *Omalisus* but it differs from *Omalisus* in the shape of male genitalia (Figs 28–35) which lacks the outwardly hooked apices of the parameres, in the small body size, the longer prosternum and the very sharp lat-



Figs 34–38. Male genitalia, ventrally. 34. *Phaeopterus unicolor*. 35. *Ph unicolor*; the holotype of *P. minutus*. 36–37. *Thilmanus obscurus*. 38. *Th. laticeps*. Scales = 0.1 mm.

eral pronotal keels that reach the frontal margins of the pronotum. *Thilmanus* has similarly shaped male genitalia, but has much smaller body than *Phaeopterus*, absent or very inconspicuous pronotal keels and very short prosternal process.

Redescription. – Male. Body small, 3.1–3.8 mm (n=10), slightly dorso-ventrally flattened, parallel-sided, well sclerotized. Head small, including eyes narrower than frontal margin of pronotum, with prominent but flat antennal tubercles separated frontally by groove. Surface of cranium roughly sculptured, sometimes with shiny part in vertex. Eyes hemispherically prominent, maximum eye diameter 0.61 times interocular distance. Antennae filiform, antennomere 1 pear-shaped, antennomere 2 longer than antennomere 3, antennomere 2 pear-shaped, antennomere 3 triangular, antennomere 4 longer than combined length of antennomeres 2 and 3, antennomeres 4–10 subequal in length, antennomere 11 longer. Clypeus apparently concave, labrum small, rounded at apex, membranous apically, mandibles long, slender, curved. Maxillary palpi with very small palpomere 1, apical palpomere longest, narrowed to apex. Labial palpi tiny, apical palpomere pointed. Pronotum flat, wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided in frontal two thirds of length, posterior angles robust, projected obliquely backwards, disc roughly sculptured at lateral margins, rather shiny, sparsely sculptured in middle part, sculptured lateral and shiny middle area separated by sharp keel attached to posterior and anterior margins of pronotum. Prosternum long, 1.43 times wider at frontal margin than long at shortest part, with short, slender prosternal process, mesosternum with straight frontal margin. Elytra parallel-sided, with ten rows of round punctures which form continuous costae, flat between elytral suture and strongly elevated costa 6 in frontal half of elytra, much less conspicuous apically, outer part forms pleura. Legs slender, slightly compressed, trochanters slender, tarsi with five tarsomeres. Male genitalia as in Figs 34–35. Female. Unknown.

Distribution. – Italy (Roma, Naples, Salerno, the Elba Island), Corsica.

Biology. – No information is available on the biology of *Phaeopterus*. Almost all studied specimens were collected at least 100 years ago and none of them is accompanied by detailed locality data.

Only one specimen was recently collected in the Elba Island by sifting. As all specimens in the studied collections are males and the incomplete metamorphosis is known in the related genus *Omalisus* the female neoteny is expected also in *Phaeopterus*.

Taxonomic discussion. – *Phaeopterus* is given generic status on the basis of several differences in both external morphology and shape of male genitalia. *Phaeopterus* and *Omalisus* share the elevated elytral costa 6 and the lateral keels at margins of pronotum, but they differ in the expression of these characters. The male genitalia of *Phaeopterus* resemble more those of *Thilmanus* than *Omalisus* (Figs 28–32 and 34–38) and the later genera share also the triangular shape of antennomere 3.

Crowson (1972) discussed the position of *Phaeopterus* and its potential generic status but he studied *Phaeopterus graecus* Pic, 1901 which has been recently transferred to the genus *Euanoma* in Drilidae (Kundrata & Bocak 2007). The concept of the genus *Phaeopterus* is considerably changed after another species, *Omalisus (Phaeopterus) nigricornis* Reitter, 1881 is combined with *Euanoma*; *O. (Phaeopterus) flavangulus* Späth, 1898 is proposed a junior subjective synonym of the previous species; and *O. (Phaeopterus) minutus* Pic, 1938 is proposed to be a junior subjective synonym of *Phaeopterus unicolor*. These taxonomic acts render *Phaeopterus* monotypic.

***Phaeopterus unicolor* Costa, 1857**

(Figs 18, 34–35)

Phaeopterus unicolor Costa, 1857: 220.

Homalisus minutus Pic, 1938: 13, syn. n.

Type material. – 1 male, holotype of *Phaeopterus minutus* Pic, Poggio Cavallo, dint. Grosseto, iv. 1899 (MHNP).

Differential diagnosis. – *Phaeopterus unicolor* is the only species placed in the genus and it is easily distinguishable from other omalids by the body size and colouration.

Redescription. – For redescription see *Phaeopterus* above.

Measurements. – BL 3.7 mm, WH 0.99 mm, PL 0.56 mm, PW 0.86 mm, Ediam 0.20 mm, Edist 0.33 mm.

Type locality. – Italy (Naples).

Distribution. – Southern part of the west coast of Italy, the Elba Island, and Corsica.

Material examined. – 1 male, PT [paratype of *P. minutus*], coll. Grenier (without further data), *P. unicolor* Costa, det. M. Pic (MHNP). FRANCE: Ajaccio, 1 male, Desbroch leg., coll. Bourgeois (MHNP); Aj., 1 male, (without further data), *Phaeopterus unicolor* Costa, det. M. Pic (MHNP); Corsica, 2 males, coll. Stierlin (DEIC); Corsica, 1905, Bocognano, 1 male, coll. O. Leonhard, Gangelbauer det. (DEIC); Corsica, 1 male (MZMB); ITALY: Umgbg. Salerno, 15.–21. 5. 1903, 1 male, Fratte leg., *Phaeopterus minutus* Pic, det. M. Pic (MHNP); Roma, 1 male, coll. Strasser (DEIC); 1 male, Roma, coll. Strasser (DEIC); Italia, Isola di Elba, Monte Perone, 600–700 m, 42.46N, 10.12E, 28. iv. 2007, 1 male, M. Geiser leg. (MGCB).

Taxonomic discussion. – Both names *P. unicolor* and *P. minutus* are based on specimens collected in Italy. We studied specimens from several localities along the Western coast of Italy and we found that all specimens belong to one species, although they were identified by M. Pic as *P. unicolor* and *P. minutus*. Therefore, we consider *P. minutus* to be a junior objective synonym of *P. unicolor*. Additionally, we have not found any character separating the allopatric populations from Italy and Corsica. We suppose that *P. unicolor* populations could have been connected during Quaternary when Italy, Sardinia and Corsica were repeatedly connected by dry land (Cherchi & Montadert 1982).

Remark. – The Costa's collection was not preserved (Horn *et al.* 1990) and the type of *P. unicolor* is probably destroyed. The identity of the species is clear and therefore we do not designate a neotype.

Genus *Thilmanus* Gemminger, 1869

(Figs 20, 26, 36–38)

Thilmanus Gemminger, 1869: 1863.

Type species. – *Thilmanus obscurus* Baudi, 1872

Differential diagnosis. – *Thilmanus* and *Phaeopterus* share the parameres without the outwardly hooked apices and the shape of the basal antennomeres. *Thilmanus* is easily recognizable in Omalisidae by its tiny, slender body (1.9–3.1 mm, n=51), very soft elytra with an irregular structure, and lacking longitudinal carinae on pronotum. Although sometimes classified with Lycidae (Crowson 1972, Kazantsev 2005) or Drilidae (Kazantsev & Medvedev 1992), *Thilmanus* differs from Lycidae due to the 7 abdominal segments and from Drilidae by the long prosternum, male genitalia, and structure of the elytra.

Redescription. – Male. Body tiny, 1.9–3.1 mm (n=51), dorso-ventrally flattened, slender, parallel-sided, feebly sclerotized. Head small, including eyes narrower than frontal margin of pronotum, with strong antennal tubercles separated by long, deep groove. Surface of cranium roughly sculptured. Eyes smaller than interocular distance, hemispherically prominent. Antennae *filiform*, round in cross section, antennomere 1 pear-shaped, antennomere 2 longer than 3, antennomere 2 pear-shaped, antennomere 3 triangular, antennomere 4 slightly shorter than combined length of antennomeres 2 and 3, antennomeres 4–10 subequal in length, antennomere 11 longer. Clypeus apparently concave, labrum small, rounded at apex, mandibles long, slender, curved. Maxillary palpi with very small palpomere 1, apical palpomere longest, narrowed pointed. Labial palpi tiny, very feebly sclerotized, apical palpomere pointed. Disc of pronotum convex, pronotum wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided in frontal two thirds of length, posterior angles robust, projected obliquely backwards, disc roughly sculptured at lateral margins, more shiny in middle part, without any keels. Elytra parallel-sided, with irregular sculpture, without any costae. Legs slender, slightly compressed, trochantalia long, tarsi with five tarsomeres. Male genitalia as in Figs 36–38. Female. Unknown.

Distribution. – *Thilmanus* is recorded from the very restricted range in the Western Mediterranean. The two known species occur allopatrically in Corsica plus Sardinia and the French Mediterranean coast (Banyuls sur Mer), respectively.

Biology. – No information is available on the biology of *Thilmanus*. All specimens available for the present study were collected in the 19th and the beginning of the 20th century and they usually bear very imprecise locality data. We do not know in most cases even the altitude where these specimens were collected. Only a few specimens from Sardinia bear more detailed information pointing to the high altitude mountain areas of Mt. Genargentu in environs of Aritzo. Altogether several dozen specimens were found in the museum collections and as all of them were males female neoteny is expected in this genus.

Taxonomic discussion. – Two morphologically very similar species are classified in *Thilmanus*

and the only reliable diagnostic characters are in their male genitalia. Similarly with an array of taxonomically diverse taxa of animals (Caccone & Sbordoni 2001; Caccone *et al.* 1994), two closely related *Thilmanus* species have allopatric distribution with *T. obscurus* occurring in Sardinia and Corsica and *T. laticeps* in Southern France. Because the potential for dispersal of all beetles with neotenic females is extremely low, the present distribution of *Thilmanus* can be related to the Oligocene detachment of the Corsica-Sardinia microplate from the Iberian plate and its movement towards the Italian peninsula (Cherchi & Montadert 1982, Boccaletti *et al.* 1990). However, this possible ancient separation of *Thilmanus* spp. is contradicted by their low morphological differentiation.

***Thilmanus laticeps* Pic, 1913, stat. n.**

(Fig. 38)

Thilmanus longicollis var. *laticeps* Pic, 1913: 185.

Type material. – Holotype, PYR. OR. Banyuls/M, A Hustache (MHNP).

Differential diagnosis. – *T. laticeps* is close to *T. obscurus* in structure of the basal part of parameres (Figs 36 – 38), but *T. laticeps* has a short, transverse groove in the middle part of internal margin of the parameres (Fig. 38).

Redescription. – Male. – Body tiny, 2.9 mm (n=1), dorso-ventrally flattened, very slender, parallel-sided. Body dark brown, apices of elytra darker. Head small, with strong antennal tubercles separated by long, deep groove. Surface of cranium roughly sculptured. Eyes hemispherically prominent, eye distance 1.26 times maximum eye diameter. Antennae *filiform*, antennomere 1 pear-shaped, antennomere 2 longer than 3, antennomere 2 pear-shaped, antennomere 3 triangular, antennomere 4 0.94 combined length of antennomeres 2 and 3, antennomeres 4–10 subequal in length, antennomere 11 longer. Disc of pronotum convex, pronotum 1.65 wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided in frontal two thirds of length, posterior angles projected obliquely backwards, disc roughly sculptured at lateral margins, more shiny in middle part, without keels. Elytra parallel-sided, slender, 3.45 times longer than combined width at humeri, with irregular sculpture, without any costae. Legs slender, slightly compressed. Male genitalia as in Fig. 38. Female. Unknown.

Measurements. – BL 2.9 mm, WH 0.67 mm, PL 0.37 mm, PW 0.61 mm, Ediam 0.19 mm, Edist 0.24 mm.

Type locality. – France (Banyuls sur Meer, Département Pyrénées Orientales, France).

Distribution. – The species is known only from a single male specimen collected in Southern France at the foothills of the Eastern Pyrenees (Pic 1913).

Taxonomic discussion. – *T. laticeps* is given the full species status considering the morphological differentiation of male genitalia and the presumed ancient isolation of populations from Eastern Pyrenees, Sardinia and Corsica.

***Thilmanus obscurus* Baudi di Selve, 1872**

(Fig. 36, 37)

Thilmanus obscurus Baudi di Selve, 1872: 96.

= *Thilmanus fuscus* Baudi di Selve, 1872: 97 (a junior objective synonym).

Thilmanus longipennis Pic, 1912: 41, syn. n. (a junior subjective synonym)

Type material. – Holotype of *Thilmanus longipennis* Pic, Sargidae, Lorgonais, Dr. Kretaise (without further data) (MHNP);

Differential diagnosis. – The species of *Thilmanus* cannot be distinguished without a study of male genitalia. *O. obscurus* is characterized by a simple inner margin of the paramerae (Figs 36, 37).

Redescription. – Male. Body tiny, 1.9 – 3.1 (n=50), dorso-ventrally flattened, very slender, parallel-sided. Body dark brown, elytra lighter than body, their apices darker. Head small, including eyes narrower than frontal margin of pronotum, with strong antennal tubercles separated by long, deep groove. Surface of cranium roughly sculptured. Eyes hemispherically prominent, eye distance 1.32 times maximum eye diameter. Antennae *filiform*, antennomere 1 pear-shaped, antennomere 2 longer than 3, antennomere 2 pear-shaped, antennomere 3 triangular, antennomere 4 0.93 combined length of antennomeres 2 and 3, antennomeres 4–10 subequal in length, antennomere 11 longer. Disc of pronotum convex, pronotum 1.5 wider than length at midline, frontal margin slightly concave, lateral margins parallel-sided in frontal two thirds of length, posterior angles robust, projected obliquely backwards, disc roughly sculptured at lateral margins, more shiny in middle part, without keels. Elytra parallel-sided,

very slender, 3.6 times longer than combined width at humeri, with irregular sculpture, without any costae. Legs slender, slightly compressed. Male genitalia as in Figs 36, 37. Female. Unknown.

Measurements. – BL 3.05 mm, WH 0.73 mm, PL 0.41 mm, PW 0.61 mm, Ediam 0.19 mm, Edist 0.25 mm.

Type locality. – Sardinia.

Distribution. – Sardinia, Corsica.

Material examined. – FRANCE, Corsica: 5 males, Coll. Leonhard (DEIC); 4 males, (without further data) (MHNP); 1 male, 1880, Reitter (without further data) (LMBC); 3 males, v. 1879 (NHMW); 1 male, Reitter (NHMW); 1 male, Collectio Kaufmann (NHMW); 2 males, Collect. Miller (without further data) (NHMW); 1 male, (HNMW); 1 male, 1905, Bocognano, coll. O. Leonhard (DEIC); 3 males, coll. Rölph (DEIC); 2 males, Coll. Kraatz (DEIC); 7 males, coll. Stierlin (DEIC); 2 males, Coll. Letzner (DEIC); 1 male Baudi, 5659 (DEIC); 1 male, 5670, coll. Kraatz (DEIC); 1 male, Reitter (DEIC), 1 male, Bruck (DEIC); 1 male 18Db, coll. Mazura (without further data) (MZMB); 3 males, Coll. Greiner (ZMBC); 1 male, Reitter (ZMBC); ITALY, Sardinia: 3 males, Arizzo, Mte Genargentu, Geo. C. Kruger, coll. O. Leonhard (DEIC); 1 male, M. Sette Fratelli, S. O. Sard., Krüger, Coll. Leonhard (DEIC); 1 male, Sorgono, A. H. Krausse, Coll. Franklin Miller (DEIC); 2 males, Gené (ZMBC).

Variability. – Some variability was found in the shape of male genitalia as illustrated in Figs 36 and 37, but we did not find any reliable character which would enable to define separate groups of populations.

Remark. – The holotype of *T. obscurus* was not available for study from Baudi's collection in the Natural History Museum in Torino is not accessible for research. Fortunately, only a single *Thilmanus* species occurs in Sardinia and Corsica and there is no doubt about its identity. Additionally, we found in the collection of the Zoological Museum of the Humboldt University in Berlin two specimens with locality data "Sard. Gené" and these specimens may belong to the series collected by Prof. Gené in Sardinia from which F. Baudi described *Thilmanus obscurus* (see Baudi, 1872). *T. longipennis* Pic, 1912 was described from Sardinia too and is proposed to be a junior subjective synonym of *T. obscurus* as we did not find any reliable morphological difference between available specimens.

Species excluded from the family Omalisidae *Euanoma nigricornis* (Reitter, 1881) comb. n.

(Fig. 33)

Omalisus nigricornis Reitter, 1881: 220.

Omalisus flavangulus Späth, 1898: 657 - syn. n.

Type material. – Holotype of *O. nigricornis*, male, Dalmatien, Ragusa [=Dubrovnik], Reitter (BMNH). Holotype of *O. flavangulus*. Male, Portoré [=Kraljevica], Späth (NHMW).

Differential diagnosis. – *P. nigricornis* is the only representative of the genus *Euanoma* occurring in Croatia and Herzegovina and it has very characteristic male genitalia with very wide parameres (Fig. 33) and phallus.

Redescription. – Male. Body medium-sized, 5.3 – 7.9 (n=7), elongate, dorsoventrally flattened. Thorax ventrally, abdomen and antennae dark brown; head light brown, pronotum and elytra testaceous. Head hypognathous, free, only slightly retracted into pronotum, head including eyes almost as wide as pronotum at frontal margin, cranium with inconspicuous antennal sockets, with shallow longitudinal depression between weak antennal sockets. Eyes hemispherically prominent, interocular distance 1.46 times eye diameter. Maxillary palpi 4-segmented, basal palpomere very short, transverse, palpomere 2 3.1 times longer than palpomere 1, widened to apex, palpomere 3 short, transverse, palpomere 4 longer than palpomere 2, apex obliquely cut. Labial palpi tiny, 3-segmented, apical palpomere similar in shape to those on maxilla. Antennae robust, filiform, reaching one third of elytral length, narrowed to apex, antennomeres 2 and 3 subequal in length, their combined length shorter than antennomere 4. Pronotum flat, 1.22 times wider than length at midline, widest at base, surface of disc matt, margins coarsely punctured, punctures at margins separated by distance approximately equal to puncture diameter. Entire pronotal disc with sparse, erect, long setae. Posterior angles sharp, prominent; posterior margin bisinuate or widely rounded, lateral margins sinuate, pronotum narrower in front of posterior angles. Anterior margin straight. Prosternum long, without apparent prosternal process. Scutellum small, simply rounded at apex. Elytra very slightly widened posteriorly, widest in apical third, almost parallel-sided, shiny, with irregular rows of punctures and sparse, erected pubescence. Legs slender, slightly compressed. Trochanter robust, femur attached apically. Male

genitalia with moon-shaped phallobase, phallus strong, longer than parameres, widest at base (Fig. 33). Female unknown.

Measurements. – BL 7.0 mm, WH 1.86 mm, PL 1.17 mm, PW 1.43 mm, Ediam 0.45 mm, Edist 0.68 mm.

Remark. – *E. nigricornis* shares all characters with other *Euanoma* species (Kundrata & Bocak 2007) and without doubt belongs to this genus which is classified in Drilidae. Among others, all species of *Euanoma* do not have longitudinal lateral keels in the pronotum and they have at most only very inconspicuous and weak longitudinal costae in the elytra. We studied all available specimens of *O. flavangulus* and *E. nigricornis* including holotypes and we have not found any character which would separate them. There is variable colouration of the pronotum with dark brown to black in the holotype of *O. flavangulus* and light brown in the holotype of *E. nigricornis*. These differences are not sufficient for the separation of the species as intermediate colouration was found in other specimens.

Distribution and biology. – Only seven specimens are known, six from the Adriatic coast of Croatia and one from Herzegovina. All specimens were collected about a hundred years ago and there are not available any recently collected specimens. The biology of the species is unknown.

Other material examined. – BOSNIA AND HERZEGOVINA: Igar Thal, 1 male, V. Zoufal leg. (MZMB). CROATIA: Sušak bei Fiume [=Rijeka], 1 male, Collectio Kaufmann (NHMW); Gobanz, 1 male, Velebrt leg. (NHMW); Ragusa [=Dubrovnik], 1 male, Kaufmann leg. (identified as *O. nigricornis*) (NHMW); Tapan, 1 male, Dr. J. Fleischer leg. (NHMP).

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