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To Maria,
with thanks
Jacek

On the Subgeneric Division of the Genus *Chaetonotus* Ehrenberg (Gastrotricha)

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Abstract. New subgeneric division of *Chaetonotus* is proposed, mostly basing on reconstruction of cuticular covering evolution. The largest subgenus *Euchaetonotus* Schwank, 1990 is redefined and its name replaced by *Chaetonotus* s. str. The subgenera *Bifasciculatella* Schwank, 1990 and *Diversichaetatella* Schwank, 1990 are rejected and three new subgenera *Primochaetus*, *Captochaetus* and *Marinochaetus* are established. New or emended diagnoses of all valid subgenera are given.

Key words: Gastrotricha, Chaetonotidae, *Chaetonotus*, systematics.

INTRODUCTION

The family *Chaetonotidae* is one of the most successful evolutionary branches of gastrotrichs. It includes about a half of the gastrotrich species known so far and $\frac{6}{7}$ of those belonging to the order *Chaetonotida*. This abundance of species is mostly a result of the extraordinary differentiation of its largest genus *Chaetonotus* Ehrenberg. The genus assembles 177 species hitherto described, commonly occurring in various fresh water environments and in the sea.

Both the great number and diversity of the species belonging to *Chaetonotus* and practical considerations justify introducing the subgeneric division of the genus. The first division of *Chaetonotus* was pro-

posed by Remane (1927, 1936) who has established the subgenus *Ch.* (*Zonochaeta*) and the groups of species *maximus*, *bogdanovii*, *formosus*, *schultzei*, *spinulosus*, *uncinus* and *simrothi*. Full division of the genus into subgenera was proposed by Schwank (1990). He has accepted the subgenus *Ch.* (*Zonochaeta*) and raised all the species-groups, except for the *simrothi* group, to the subgeneric level, giving them the names, respectively, *Euchaetonotus*, *Diversichaetatella*, *Bifasciculatella*, *Schizochaetonotus*, *Hystricochaetonotus* and *Brevipedichaeta*. The representatives of the *simrothi* group have been included in the subgenus *Ch.* (*Euchaetonotus*).

Still having limited knowledge of the intrageneric diversity of *Chaetonotus*, Remane was conscious of the provisional character of the proposed division and of its significance practical rather than reflecting real phylogenetic relationship within the genus. Sharing his prudence, none of the further researchers have raised the Remane's groups to the subgeneric level in

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more than fifty years. Unfortunately, the subgeneric division of *Chaetonotus* finally proposed by Schwank (1990) and strictly based on the Remane's preliminary classification, might be retained only in its minor part. Having not sufficiently taken into consideration the trends occurring in evolution of *Chaetonotus*, it hardly reflects phylogenetic relationships.

The aim of the present paper is to describe the intrageneric evolutionary trends and to introduce a new subgeneric division of the genus *Chaetonotus*. An useful complement to the present considerations is the discussion on the phylogenetic relationships within the family *Chaetonotidae* as presented in my earlier paper (Kisielowski 1991) that was mostly based on new Brazilian material.

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EVOLUTIONARY TRENDS WITHIN THE GENUS CHAETONOTUS

Taking in consideration so-far available data, the most probable evolution of the cuticular structures in the genus *Chaetonotus* is as presented on Fig. 1.

As I have shown previously (Kisielowski 1991), the genus *Chaetonotus* derives directly from the genus *Lepidochaetus* Kisielowski, 1991. Consequently, the most primitive cuticular covering of the *Chaetonotus* was formed of one-lobed, rectangular scales with their anterior edges extroverted and their surfaces smooth. Those scales were armed with long, straight and thin spines, originating from their posterior extremity and each showing a delicate lateral denticle. The spines

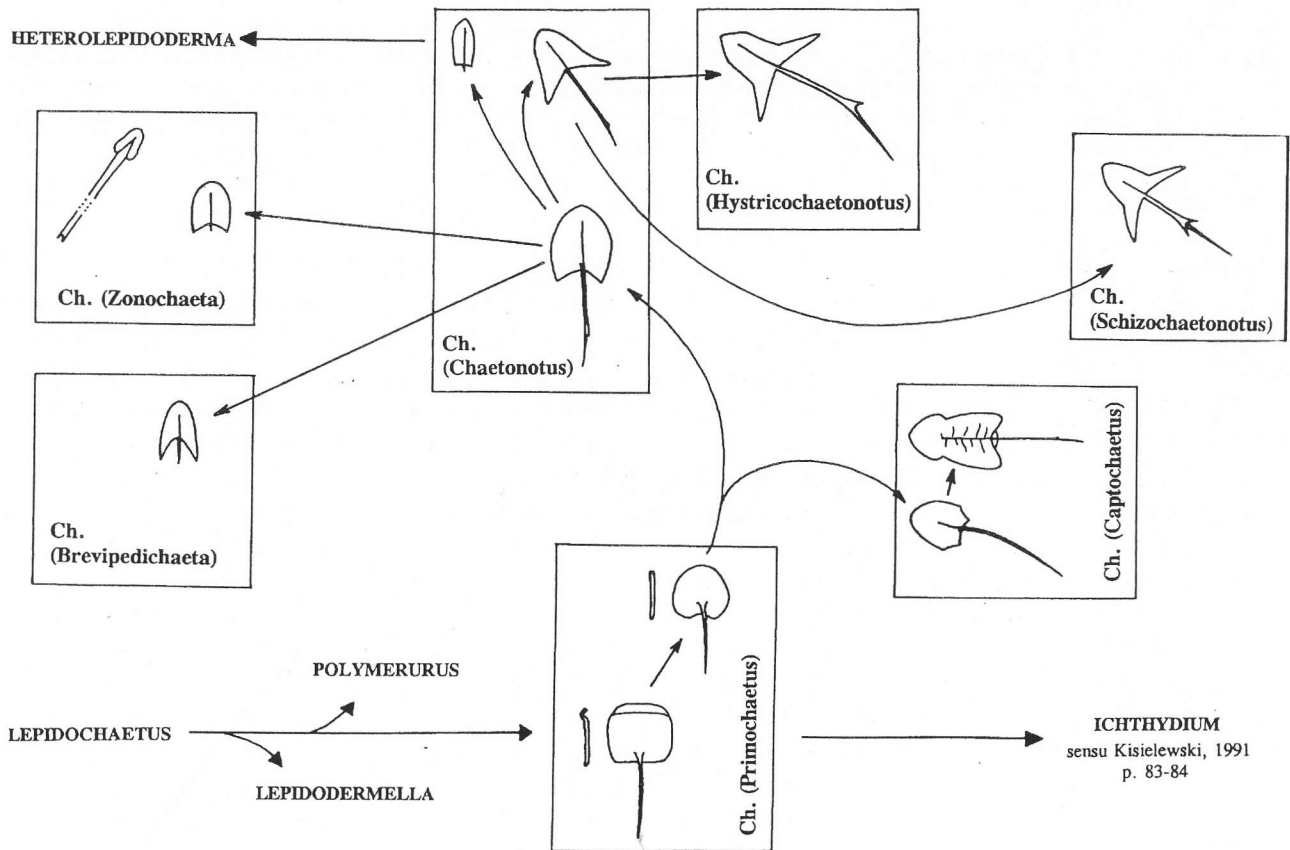


Fig. 1. The most probable evolution of the cuticular structures in the genus *Chaetonotus*

arising laterally from the furca base were the longest. Another ancestral character was the accordance, both in form and number (counted in a longitudinal row) of the dorsal scales with those on the ventral field. The further evolution of the ancestral branch of *Chaetonotus* led to the loss of the anterior edge extroversion of scales and the modification of the scale shape into more rounded. Also the spine shape was modified into thicker and more curved, often shorter and lacking lateral denticle. The ancestral set of body covering characters corresponds best to that of the species *Ch. heideri* Brehm, 1917 and *Ch. acanthodes* Stokes, 1889. All the species of *Chaetonotus* showing one-lobed scales without clear posterior notches and having spines borne near posterior edges of scales I propose to include in the subgenus *Ch. (Primochaetus)* subgen. nov.

Already at the early stage of evolution of this primitive subgenus the tendency has appeared in certain body regions, especially at the postero-median part of trunk dorsally and laterally, towards a sharp spine elongation. It is however not justified enough to exclude from this subgenus, on the basis of this only feature, such species as *Ch. acanthocephalus* Valkanov, 1937 or the more so primitive one as *Ch. acanthodes*. The above mentioned tendency was consolidated in the subgenus *Ch. (Zonochaeta)* Remane. Separate position of that subgenus is justified by other distinct features like strongly modified shape of scales, especially of those bearing conspicuous "band" spines. These spines themselves are also considerably specialized, clearly differing from those distributed along the rest of the body. Also the ventral field scales usually are smaller, more numerous and show modified shape in comparison with the dorsal ones.

Further evolution of the scale form led toward narrower scales with posterior notches. This process was accompanied by formation of the longitudinal scale keel and often by the reduction of spine length. The accordance in form and number (counted in a longitudinal row) of dorsal scales with those from the ventral field became weaker and finally disappeared. The branch of *Chaetonotus* that corresponds to this trend is the most abundant in species and very variable morphologically. I propose to consider it as the subgenus *Chaetonotus s. str.* The name *Euchaetonotus* introduced by Schwank (1990) referred to an obviously polyphyletic group, joining representatives of the genus *Lepidochaetus* and at least of

three subgenera of *Chaetonotus*, i.e. *Chaetonotus s. str.*, *Ch. (Captochaetus)* and *Ch. (Marinochaetus)* (see below). The subgenus *Chaetonotus s. str.* should include the species previously classified in the Remane's species group *formosus* ranked as the subgenus *Ch. (Bifasciculatella)* by Schwank (1990). The median head plates, i.e. the anterior pleurae, vary in size and position even within the groups of very close species (compare *Ch. polyspinosus* and *Ch. aff. polyspinosus* III in Kisielewski, 1991). In function of that, they laterally project or not, giving impression of, respectively, five- or three-lobed head. Such a difference is obviously insignificant phylogenetically, giving no reason to distinguish a separate subgenus only on that basis.

Distinctly three-lobed scales derived from one-lobed ones having posterior notches. Occurrence of the three-lobed scales almost always coincides with the presence of lateral denticles on spines. It is worth of mention that many species with three-lobed scales show almost constant pattern of scale distribution, i.e. 13–15 longitudinal alternating rows, 13–15 scales in each of them. The next step in the evolution of this branch was substantial increase in size of certain postero-median dorsal spines, often causing reduction or even vanishing of the remaining spined scales. The described branch well corresponds to the Remane's *spinulosus* group, which has been recently raised to the subgeneric level by Schwank (1990) under the name *Hystricochaetonotus*.

Still unclear is the status of the former *schultzei* group, especially the relationship between the only freshwater species *Ch. schultzei* Mecnikow, 1865 and rather large and strongly diversified marine branch. The present knowledge of the group does not oppose, however, to treating it as a subgenus, for which Schwank (1990) has proposed the name *Schizochaetonotus*.

Considering the *uncinus* group as subgenus, viz. *Ch. (Brevipedichaeta)* Schwank, 1990, was problematic, but including here the species *Ch. brachyurus* Balsamo, 1981 seems to be a mistake. The adhesive tubes could vanish in any *Chaetonotidae* line (compare the origin of the *Dasydytidae*, *Neogosseidae* and *Undulinae* – see Kisielewski, 1991) and the body covering of *Ch. brachyurus* is quite different from that occurring in the species *Ch. uncinus* Voigt, 1902 and *Ch. sudeticus* Kisielewski, 1984. After excluding the species *Ch. brachyurus* from *Ch. (Brevipedichaeta)*, I propose to provisionally retain its subgeneric status. It is justified

by occurrence of unique in *Chaetonotus* strong hook-like subterminal spines as well as similar shape and distribution of scales. I have found some further, not yet described, species belonging to this subgenus in Brazilian tropical waters. Although basal parts of its caudal appendages are not reduced, the presence of strong terminal spines and rudimentary adhesive tubes makes it justified to include the species *Ch. caudal-spinosus* Visvesvara, 1965 in the same subgenus.

Probably some representatives of the subgenus *Ch. (Primochaetus)* still having regularly one-lobed scales gave rise to a marine line of *Chaetonotus* characterized by round or oval scales without any trace of posterior notches. The most peculiar feature of this line is central or even anterior position of the spine base on the scale. All the well-known species of this new subgenus, for which I propose the name *Ch. (Marinochaetus)* subgen. nov., show naked ventral field, often provided however with one or two pairs of terminal scales.

Paradoxically, the only Remane's species group of *Chaetonotus* not recognized by Schwank (1990) as a subgenus, i.e. the *simrothi* group, decidedly does merit such a status. This subgenus, which I name *Ch. (Captochaetus)* subgen. nov., can be distinguished from the others on the basis of both anatomical and morphological characters. The subgenus includes large and very large predatory gastrotrichs. Their mouth rings consist of one-element lamellae and show extraordinary extensibility. Similarly extensible is the pharynx, being wide and lacking bulbs. One more character in common is the very large hypostomion with strong transverse furrow. Apparently, it allows to immobilize a prey (often only twice shorter than the predator) during swallowing. The subgenus in question should be rather ancient, which is suggested by wide variety of scale shapes.

DIAGNOSES OF SUBGENERA

Ch. (Chaetonotus) s. str.

Chaetonotus of body length 80–370 μm . Scales one-lobed, with their anterior edges not extroverted and with posterior notches; small postero-lateral scale lobes occasionally occur. Scales axially keeled along at least a half of their length. Spines arising near posterior edge of scales, without or with single lateral denticle, all of equal length or becoming gradually

longer towards the mid-trunk or trunk rear. A group of spines conspicuously longer than others never occurs on the trunk but can occasionally be present at the furca base. An area with shorter spines or even without them often occurs on dorsal side of trunk rear. Ventral field covering differs in scale distribution and usually also in scale form from that of dorsal body side. Posterior and often anterior pharynx thickening marked. Freshwater, brackishwater and marine. Benthic, interstitial and periphytic, rarely semiplanktonic.

66 species: *Ch. larius* (Müller, 1786) Ehrenberg, 1838 (type species); *Ch. aculeatus* Robbins, 1965; *Ch. aegilonensis* Balsamo, Todaro & Tongiorgi, 1992; *Ch. alatus* Schwank, 1990; *Ch. alni* Nesteruk, 1991; *Ch. angustus* Schrom, 1972; *Ch. apechochaetus* Hummon, Balsamo & Todaro, 1992; *Ch. benacensis* Balsamo & Fregni, 1995; *Ch. bifidispinosus* Tret'akova, 1991; *Ch. breviacanthus* Kisielowski, 1991; *Ch. brevispinosus* Zelinka, 1889; *Ch. christianus* Schwank, 1990; *Ch. condensus* Mock, 1979; *Ch. daphnes* Balsamo & Todaro, 1995; *Ch. disiunctus* Greuter, 1917; *Ch. dybowskii* Jakubski, 1919; *Ch. elegans* Konsuloff, 1921; *Ch. fluviatilis* Balsamo & Kisielowski, 1986; *Ch. furcatus* Kisielowski, 1991; *Ch. greuteri* Remane, 1927; *Ch. heterochaetus* Daday, 1905; *Ch. heterospinosus* Balsamo, 1977; *Ch. hirsutus* Marcolongo, 1910; *Ch. hoanicus* Schwank, 1990; *Ch. illiesi* Schwank, 1990; *Ch. intermedius* Kisielowski, 1991; *Ch. laroides* Marcolongo, 1910; *Ch. linguaeformis* Voigt, 1902; *Ch. lobo* Kisielowski, 1991; *Ch. longisetosus* Preobrazenskaja, 1926; *Ch. lunatospinosus* Balsamo, 1980; *Ch. maximus* Ehrenberg, 1838; *Ch. microchaetus* Preobrazenskaja, 1926¹; *Ch. minimus* Marcolongo, 1910; *Ch. mitraformis* Greuter, 1917; *Ch. multispinosus* Grünspan, 1908; *Ch. naiadis* Balsamo & Todaro, 1995; *Ch. napoleonicus* Balsamo, Todaro & Tongiorgi, 1992; *Ch. oculatus* Schwank, 1990; *Ch. oculifer* Kisielowski, 1981; *Ch. odontopharynx* Grosso & Draha, 1986; *Ch. oplites* Balsamo, Fregni &

¹The original description of the species is complete enough to consider further findings by Kisielowski (1979) and Balsamo (1983) as referring to the same species. The name *Ch. balsaminus* Schwank, 1990 should be therefore considered a junior synonym of *Ch. microchaetus* Preobrazenskaja, 1926.

Tongiorgi, 1994; *Ch. parafurcatus* Nesteruk, 1991; *Ch. paucisquamatus* Kisielowski, 1991; *Ch. pawlowskii* Kisielowski, 1984²; *Ch. pilaga* Grosso, 1982; *Ch. polyspinosus* Greuter, 1917 (*Ch. annulatus* Martin, 1990 syn. nov.); *Ch. poznaniensis* Kisielowski, 1981; *Ch. pratensis* Schwank, 1990; *Ch. pseudopolyspinosus* Kisielowski, 1991; *Ch. puniceus* Martin, 1990; *Ch. pusillus* Daday, 1905; *Ch. rarispinosus* Roszczak, 1935; *Ch. remanei* Schwank, 1990; *Ch. sanctipauli* Kisielowski, 1991; *Ch. schoepferi* Thane-Fenchel, 1970; *Ch. scutatus* Saito, 1937; *Ch. siciliensis* Hummon, Balsamo & Todaro, 1992; *Ch. silvaticus* (Varga, 1963) Kisielowski, 1991; *Ch. similis* Zelinka, 1889; *Ch. sphagnophilus* Kisielowski, 1981; *Ch. tempestivus* Mock, 1979; *Ch. triacanthus* Todaro, 1994; *Ch. vellosus* Martin, 1990; *Ch. ventrochaetus* Kisielowski, 1991; *Ch. venustus* d'Hondt, 1967.

Ch. (Primochaetus) subgen. nov.

Etymology. From the Latin "primus" – first and the Greek "khaite" – long hair, referring to the most primitive position in the genus.

Chaetonotus of body length 90–280 μm . Scales one-lobed, with their anterior edges extroverted or flat, without keels. Posterior edges of scales notchless or at most with shallow and rounded deepness. Spines arising near posterior edges of scales, thick and straight, rarely curved basally, without or with single lateral denticle. All spines of equal length or becoming gradually longer towards the mid-trunk. One or two pairs of conspicuously longer spines often occur latero-terminally but never dorso-terminally. Ventral field scales usually agree in form, number and distribution with those from respective part of dorsum.

²The form *Ch. aff. pawlowskii*, described by me (Kisielowski 1984), differs from *Ch. pawlowskii* only in having longer spines, showing the same form of pharynx, hypostomion and head. It seems that the species is differentiated geographically as I recently found a still different form of *Ch. pawlowskii* in Israel (not yet described). Schwank (1990) has raised the form *Ch. aff. pawlowskii* to the specific rank, introducing the name *Ch. polonicus*. It could be more proper to regard all these different forms as subspecies. The nominative subspecies should therefore be named *Ch. pawlowskii pawlowskii* Kisielowski, 1984, whereas the form "*Ch. aff. pawlowskii*" (= *Ch. polonicus* Schwank, 1990) should get the name *Ch. pawlowskii polonicus* Schwank, 1990.

Posterior and often anterior pharynx thickening marked. Freshwater. Benthic and periphytic.

21 species: *Ch. acanthodes* Stokes, 1887 (type species); *Ch. acanthocephalus* Valkanov, 1937³; *Ch. armatus* Kisielowski, 1981; *Ch. arquatus* Voigt, 1903; *Ch. brachyurus* Balsamo, 1981; *Ch. chuni* Voigt, 1901; *Ch. cordiformis* Greuter, 1917; *Ch. dubius* Daday, 1905; *Ch. erinaceus* Daday, 1905; *Ch. heideri* Brehm, 1917; *Ch. heteracanthus* Remane, 1927; *Ch. macrolepidotus* Greuter, 1917⁴; *Ch. mutinensis* Balsamo, 1977; *Ch. ploenensis* Voigt, 1909; *Ch. rectaculeatus* Kisielowska, 1981; *Ch. rotundus* Greuter, 1917; *Ch. scoticus* Schwank, 1990; *Ch. scutulatus* Martin, 1990; *Ch. soberanus* Grosso & Drahg, 1983; *Ch. tenuis* Grünspan, 1908; *Ch. tenuisquamatus* Grosso, 1982.

Ch. (Hystricochaetonotus) Schwank, 1990

Chaetonotus of body length 60–190 μm . Scales with three distinct lobes, one anterior and two postero-lateral, as well as with clear axial keel. Spines with a lateral denticle; occasionally denticles are lacking or two subsequent denticles occur. All spines well developed and becoming gradually longer towards the trunk rear. In some species spines more or less reduced, except for the postero-median part of trunk, where a group of conspicuous dorsal spines occurs. Posterior and often anterior pharynx thickening marked. Freshwater and rarely marine. Periphytic, benthic and interstitial.

³So far known intraspecific variability of *Ch. acanthocephalus* (see Kisielowski 1991) gives no reason to treat the form described by me under the name *Ch. aff. acanthocephalus* (Kisielowski 1981) as a distinct taxon. Therefore, its name *Ch. kisielowskii*, proposed by Schwank (1990), should be considered a junior synonym of *Ch. acanthocephalus* Valkanov, 1937.

⁴Considering the fact that two taxa previously described as separate species, viz. *Ch. macrolepidotus* Greuter, 1917 and *Ch. ophiogaster* Remane, 1927, differ only in length of spines, having in common all other important features (ventral field covering, scale form, shape of pharynx and of adhesive tubes), I find more appropriate to regard them as two subspecies of the same species: *Ch. macrolepidotus macrolepidotus* Greuter, 1917 and *Ch. macrolepidotus ophiogaster* Remane, 1927. Consequently, the names *Ch. ophiogaster intermedia* Martin, 1990 and *Ch. ophiogaster ophiogaster* Martin, 1990 should be considered junior synonyms of respectively *Ch. macrolepidotus macrolepidotus* and *Ch. macrolepidotus ophiogaster*.

29 species: *Ch. hystrix* Mecnikow, 1865 (type species); *Ch. acanthophorus* Stokes, 1888; *Ch. aemilianus* Balsamo, 1978; *Ch. anomalus* Brunson, 1950; *Ch. balsamoae* sp. nov.⁵, *Ch. decemsetosus* Marcolongo, 1910; *Ch. enormis* Stokes, 1887; *Ch. euhystrix* Schwank, 1990; *Ch. ferrarius* Schwank, 1990; *Ch. italicus* Balsamo & Todaro, 1995; *Ch. lacunosus* Mock, 1979; *Ch. longispinosus* Stokes, 1887; *Ch. lucksi* Voigt, 1958; *Ch. macrochaetus* Zelinka, 1889; *Ch. murrayi* Remane, 1929; *Ch. novenarius* Greuter, 1917; *Ch. octonarius* Stokes, 1887; *Ch. paucisetosus* Marcolongo, 1910; *Ch. persetosus* Zelinka, 1889; *Ch. polychaetus* Daday, 1906; *Ch. pungens* Balsamo, 1990; *Ch. quintospinosus* Greuter, 1917; *Ch. schlitzensis* Schwank, 1990; *Ch. spinifer* Stokes, 1887; *Ch. spinulosus* Stokes, 1887; *Ch. trichodrymodes* Brunson, 1950; *Ch. trilineatus* Valkanov, 1937; *Ch. trispinosus* Balsamo, 1990; *Ch. vargai* Rudescu, 1967.

Ch. (Zonochaeta) Remane, 1927

Chaetonotus of body length 65–235 μm . Scales one-lobed and elongated, keeled along their nearly whole length, with or without short spines. A transverse row of long simple spines (occasionally barbed or bifurcated) occurs dorsally and laterally at the anterior trunk region. Their basal scales differ in form and size from the others. Second row of conspicuous spines occasionally present also at the posterior trunk region. A pair of long lateral terminal spines always present. Posterior and often anterior pharynx thickening marked. Freshwater. Benthic and periphytic.

10 species: *Ch. succinctus* Voigt, 1902 (type species); *Ch. bisacer* Greuter, 1917; *Ch. caricicola*

Schwank, 1990; *Ch. cestacanthus* Balsamo, 1990; *Ch. dracunculus* Balsamo, 1990; *Ch. multisetosus* Preobrazenskaja, 1926; *Ch. palustris* Anderson & Robbins, 1980; *Ch. pentacanthus* Balsamo, 1981; *Ch. trichostichodes* Brunson, 1950; *Ch. voighti* Greuter, 1917.

Provisionally included: *Ch. sextospinosus* Visvesvara, 1965.

Ch. (Schizochaetonotus) Schwank, 1990

Chaetonotus of body length 125–400 μm . Pleurae and occasionally cephalion reduced. Scales one- or three-lobed, in some species fused with cuticle. Spines with two lateral denticles inserted at the same point; rarely an additional and more distally located denticle occurs. Spines all of equal length, or becoming gradually longer towards the mid-trunk or trunk rear. Posterior and anterior pharynx thickening marked. Marine and brackishwater with only one freshwater species. Benthic and periphytic.

11 species: *Ch. schultzei* Mecnikow, 1865 (type species); *Ch. atrox* Wilke, 1954; *Ch. dispar* Wilke, 1954; *Ch. hilarus* Schrom, 1972; *Ch. inaequidentatus* Kisielowski, 1988; *Ch. jucundus* Schrom, 1972; *Ch. luporinii* Balsamo, Fregni & Tongiorgi, 1996; *Ch. modestus* Schrom, 1972; *Ch. neptuni* Wilke, 1954; *Ch. serenus* Schrom, 1972; *Ch. woodi* Thane-Fenchel, 1970.

Ch. (Captochaetus) subgen. nov.

Etymology. From the Latin "captare" – to seize and the Greek "khaite" – long hair, referring to predatory mode of life and spined appearance.

Chaetonotus of body length 210–625 μm . Hypostomion large and strong, with deep transverse furrow. Scales one-lobed, with flat anterior edges and posterior notches. Spines often strongly curved basally, without or occasionally with a lateral denticle; their length slightly increases gradually towards mid-trunk. Mouth ring elements non-segmented and flattened. Pharynx wide and soft, equal in width from anterior to posterior. Freshwater. Benthic and periphytic.

7 species: *Ch. simrothi* Voigt, 1909 (type species); *Ch. arethusae* Balsamo & Todaro, 1995; *Ch. insigniformis* Greuter, 1917; *Ch. jakubskii* Roszczak, 1935;

⁵Although similar to *Ch. novenarius* Greuter, 1917, the gastrotrich found and referred to the same species by Balsamo (1983) differs from the Greuter's worm in having two subsequent lateral denticles on each of nine longest dorsal spines instead of a single one. This constant and well-visible feature is so unusual that could not be omitted by such an experienced searcher as Greuter was. The Balsamo's gastrotrich should therefore be regarded as a separate species, for which I propose the name *Ch. balsamoae* sp. nov., given in honour of the author of its first full description. All my observations referring to *Ch. anomalus* Brunson (Kisielowski 1981) and *Ch. novenarius* Greuter sensu Balsamo (Kisielowski & Kisielowska 1986, Kisielowski 1991) concern this new species, as described and figured in Balsamo, 1983.

Ch. majestuosus Grosso & Drahg, 1984; *Ch. robustus* Davison, 1938; *Ch. vorax* Remane, 1936.

4 species provisionally included: *Ch. gastrocyaneus* Brunson, 1950; *Ch. rafalskii* Kisielowski, 1979; *Ch. segnis* Martin, 1990; *Ch. tricuspидatus* Schwank, 1990.

***Ch. (Brevipedichaeta)* Schwank, 1990**

Chaetonotus of body length 185–340 μm . Caudal furca more or less reduced, with rudimentary adhesive tubes and some strong hooked spines dorsally. Freshwater. Benthic.

3 species: *Ch. uncinus* Voigt, 1902 (type species); *Ch. caudalispinosus* Visvesvara, 1965; *Ch. sudeticus* Kisielowski, 1984.

***Ch. (Marinochaetus)* subgen. nov.**

Etymology. From the Latin "marinus" – marine and the Greek "khaite" – long hair, referring to occurrence in the sea and spined appearance.

Chaetonotus of body length 85–190 μm . At least dorsal trunk scales regularly round or longitudinally oval, without axial keels and without any trace of posterior notches. Spines, which originate between the scale center and its anterior edge, are rather strong, simple or having lateral denticle. Ventral field naked except for its posterior extremity, where one or two pairs of keeled/spined scales usually occur. Posterior and often anterior pharynx thickening marked. Marine and brackishwater. Interstitial.

8 species: *Ch. mariae* Todaro, 1992 (type species); *Ch. aequispinosus* Schrom, 1972; *Ch. antipai* Rodewald, 1938; *Ch. apolemmus* Hummon, Balsamo & Todaro, 1992; *Ch. chicous* Hummon, 1974; *Ch. oligohalinus* Hummon, 1974; *Ch. sagittarius* Evans, 1992; *Ch. testiculophorus* Hummon, 1966.

Provisionally included: *Ch. oceanides* d'Hondt, 1971.

Species of *Chaetonotus* of unclear subgeneric position:

Ch. annectens Grosso & Drahg, 1991; *Ch. balticus* Remane, 1926; *Ch. dentatus* Tret'akova, 1992;

Ch. fencheli d'Hondt, 1974; *Ch. lancearis* Tret'akova, 1992; *Ch. laterospinosus* Visvesvara, 1965; *Ch. monobarbatus* Visvesvara, 1965; *Ch. montevidensis* Cordero, 1918; *Ch. parthenopeius* Wilke, 1954; *Ch. somniculosus* Mock, 1979; *Ch. tachyneusticus* Brunson, 1948; *Ch. tentaculatus* d'Hondt, 1971; *Ch. trianguliformis* Visvesvara, 1965; *Ch. variosquamatus* Mock, 1979; *Ch. vechovi* Tret'akova, 1992; *Ch. vulgaris* Brunson, 1950 (16 species).

Nomina dubia (insufficiently described species of *Chaetonotus*):

Ch. beauchampi d'Hondt, 1967; *Ch. bogdanovii* Schimkewitsch, 1886; *Ch. crassus* Preobrazenskaja, 1926; *Ch. formosus* Stokes, 1887; *Ch. pygmaeus* Schwank, 1990; *Ch. quadratus* Martin, 1990; *Ch. splendidus* Preobrazenskaja, 1926; *Ch. stagnalis* d'Hondt, 1967; *Ch. striatus* Preobrazenskaja, 1926.

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