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Review of the [*Cyphogastra* DEYR.]-supergenous (Coleoptera: Buprestidae) I. Mysteries of early evolution: *Pleiona* DEYR. and sg. *Guamia* THY.

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Introduction

My notes on *Cyphogastra* DEYR. (HOŁYŃSKI 1992a, b) were published long ago, and now, in the light of new material and new information accumulated thereafter, look badly outdated. This is especially true as regards the sg. *Guamia* THY., where virtually everything – from nomenclature and distribution, through internal taxonomy and relation to the nominotypical subgenus, to phylogenetical reconstruction – needs comments and/or correction. The aim of this paper is to summarize my present understanding of the taxonomy, biogeography and phylogeny of this excitingly interesting group. The inclusion of *Pleiona* DEYR., necessary already for the sake of completeness, introduces an intriguing evolutionary phenomenon: the paradoxical coincidence of close relationship and diametrically opposite development of morphological adaptations.

Conventions and abbreviations

Generally I follow the format adopted in the books on the **Chrysochroina** CAST. (HOŁYŃSKI 2009) and **Julodinae** LAC. (HOŁYŃSKI 2014); in particular only new taxa will be described in detail, while for those named earlier concise summaries of distinctive characters (“extended diagnoses”) will be given.

Like in my other publications (unless “corrected” by editors...), I follow the very useful conventions of applying (of course, except wordly citations, where the original form must be retained) SMALL CAPS to *all* [irrespective of context and full vs. abbreviated version: inconsistent use deprives the display of any sense!] personal family- (*not* given-) names, *italicizing* species- and genus-group names (as well as citations and words in languages different from that of the main text), and writing the suprageneric taxon-names in **Bold** [the latter is not a generally accepted custom, but is often important, as some of such names (*e.g.* of the subtribes **Buprestina** LEACH, **Melobasina** BÍLÝ or **Coraebina** BED.) are (or may easily become) “homonymous” (but valid!) with generic or subgeneric ones (*Buprestina* OBB., *Melobasina* KERR., *Coraebina* KERR.)]: we must make possibly unequivocal what we have in mind, and possibly easy for the reader to “optically” spot the “wanted” name in the (especially longer) text!

Labels of type-specimens are quoted as exactly as possible, including *italics* and *handwriting* (both represented in my text by *italics*), CAPITAL LETTERS, SMALLCAPS and framing [in case of specimens examined long ago (especially in BMNH), and now not accessible for checking, my notes may have not contained information as to such details, so the citations herein may be inexact in this respect]. Like in my other recent works, in the

enumeration of the type-material individual labels (except those added by myself) are cited in quotation mark; my own labels are not cited – according to my current custom they are two or three: white determination-label (e.g. “*Cyphogastra obsoleta* HOL. det. R. HOŁYŃSKI 1978” – the year of determination written vertically on the left); red holotype- or green paratype-label (e.g. “*Cyphogastra obsoleta* HOŁYŃSKI. HOLOTYPE” or – earlier – only a red “PARATYPE” vs. “HOLOTYPE”); and (if belonging to my collection) small white collection-label with specimen-identifying signature (e.g. “coll. RBHOŁYŃSKI BPCje”); specimens in my collection not belonging to type-series bear two (determination- and collection-) of these labels.

Collection names are abbreviated as follows:

BMNH = Natural History Museum, London, GREAT BRITAIN
 BPBM = Bernice P. Bishop Museum, Honolulu, USA
 CLB = Charles L. BELLAMY, Sacramento, USA
 KBIN = Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel, BELGIUM
 MNHN = Muséum National d’Histoire Naturelle, Paris, FRANCE
 NNHM = Nationaal Natuurhistorisch Museum, Leiden, HOLLAND
 RBH = Roman B. HOŁYŃSKI, Milanówek, POLAND;
 USNM = Smithsonian Institution: National Museum of Natural History, Washington, USA

Besides, the following terms and abbreviations are used in morphological descriptions and phylogenetic reconstructions:

dfp = “dense-and-fine punctulation” or “densely-and-finely punctulate”; refers to the type of sculpture occurring mainly in depressed areas (foveae, sulci), and consisting of fine, dense, regular punctulation on usually distinctly microsculptured background, covered with dense pubescence and frequently pulverulent

Midlateral = placed between midline and lateral margin, at *ca.* equal distance from both

Convergent/divergent = towards apex or (front) downwards

Anterolateral angle = angular meeting point between oblique truncation of apical angle and basal *ca.* $\frac{3}{4}$ of lateral margin of pronotum

Collar = narrow anteriormost “selvage” of pronotum, separated (usually only on sides) from the rest by fine furrow

Anteromedian fovea = small depression placed midlaterally just behind apical margin of pronotum

Laterobasal fossa = deep, often dfp at bottom, depression near the basal pronotal angles

Prometasternal ledge = swelling of meso-metasternal area behind sternal cavity, disrupting pro-mesosternal profile

Abdominal plaque = flattened swelling of apical part of first sternite elevated “above”, or at least meeting (in lateral aspect) at angle with, the ventral outline of 2.-5. segments

Phenun = phenetic unit: the unitary step in a transformation chain

Geocladogram = map showing simultaneously branching pattern and presumable routes of dispersal

L = length

W = width

BW = basal width

AW = apical width

H = width of head with eyes

V = width of vertex between eyes

i.l. = *in litteris* [unpublished name]

issp. = infrasubspecific name

≈ = approximately equal to

┌ ┘ = a label glued onto a more “general” one [customary in KBIN]

Systematic review

BUPRESTIDAE LEACH

BUPRESTINAE LEACH

Buprestini LEACH

Chrysochroina CAST. 1835

Chrysochroidae CASTELNAU 1835: 158

Catoxanthina JAKOBSON 1913: 778

Iridotaenini [*sic!*] TÔYAMA 1987: 5-6

Calloplastina KUROSAWA 1990: 63-64

Eucalloplastina BELLAMY 2003: 31

Remarks:

The phylogenetic reconstruction proposed earlier (HOŁYŃSKI 2009) recovered two main (**Chrysochroid** and **Paracuptoid**) and one minor, poorly substantiated (**Parataenioid**) lineages within the **Chrysochroina** CAST.; *Cyphogastra* DEYR. belongs to the **Paracuptoid lineage**, making there – together with *Pleiona* DEYR. – a well differentiated suprageneric group for which I hereby propose the term supergenus.

Abbreviated key to supergenera and genera of the Chrysochroina CAST.

- 1 (2) Scutellum hidden; or – if its narrow (narrower than 1. antennomere) apical (usually not touching pronotal base) part visible – median line of pronotum not depressed
..... **Chrysochroid lineage**
- 2 (1) Scutellum visible, wider than 1. antennal joint, broadly touching pronotal base; or – if very small and not touching base of pronotum – pronotal midline sulcate
- 3(10) Anterolateral lobes of pronotum conspicuously produced before, and making deep re-entering angle with, oblique sides of anterior margin of prosternum; if indistinct, then anal sternite without medial carina **Paracuptoid lineage**
- 4 (9) Apical emargination of labrum broader than deep, reaches at most to *ca.* midlength
- 5 (6) Abdomen not angular in profile [fig. 1]; sometimes strikingly convex and maximum height of body at end of 1. sternite, or pro-metasternal ledge conspicuous, but in such cases lateroapical margins of elytra distinctly denticulate. No trace of abdominal plaque [fig. 6] [*Paracupta* DEYR.]-supergenus
- 6 (5) Maximum height of body at apical half of 1. sternite or at anterior part of metasternum (“pro-metasternal ledge”); in doubtful cases lateroapical elytral margins smooth (except sutural denticle) [*Cyphogastra* DEYR.]-supergenus
- 7 (8) Maximum height of body at apical half of 1. sternite (“abdominal plaque” usually more or less distinct [fig. 3, 4, 5, 8, 9]) *Cyphogastra* DEYR.
- 8 (7) Maximum height of body at anterior part of metasternum (“pro-metasternal ledge” [fig. 2, 7]) *Pleiona* DEYR.
- 9 (4) Labrum almost totally divided into two lobes by deeply (at least as deep as wide) triangular apical emargination *Holynskius* ÖZD.
- 10 (3) Anterolateral lobes indistinct, anterior pronotal margin makes almost continuous line with nearly straight anterior margin of prosternum
- 11(12) Anal sternite without median carina *Iridotaenia* DEYR.
- 12(11) Anal sternite medially carinate **Parataenioid lineage**



Fig. 1. Metataenia ocellata (L.S.)



Fig. 2. Pleiona tayauti (GUÉR.)



Fig. 3. Cyphogastra taitina KERR.



Fig. 4. Cyphogastra tinianica KUR.



Fig. 5. Cyphogastra uxorismeae HOL.



Fig. 6
Metataenia ocellata (L.S.)



Fig. 7
Pleiona tayauti (G.-M.)



Fig. 8
Cyphogastra (Guamia) taitina KERR.



Fig. 9
Cyphogastra (s.str.) uxorismeae HOL.

***Pleiona* DEYR.**

Pleiona DEYROLLE 1864: 12

[type-species: *Chrysodema tayauti* GUÉRIN-MÉNEVILLE 1847]

Characters: Monotypic genus – see species description for characters and distribution.

Remarks: Ventral profile, with prominent pro-metasternal ledge and flat abdomen, resembles some representatives (sg. *Pseudocallopietus* OBB. of *Philocteanus* DEYR., several species of *Chrysochroa* DEJ.) of the **Chrysochroid lineage**, but sharply differentiates *Pleiona* DEYR. from its closest – albeit showing quite opposite adaptations – relative: *Cyphogastra* DEYR. Also arcuate lateroapical margins of elytra, with rather broadly rounded apices and no indication of “caudate” tendency, make it superficially so much more resembling some *Chrysochroa* DEJ. than any *Cyphogastra* DEYR. that it may seem astonishing why it has invariably been placed next to the latter. And nevertheless phylogenetical reconstructions (HOŁYŃSKI 2009) confirmed this traditional placement and closer examination of e.g. frontal, pronotal or prosternal structures does also support it. Thus, even though my earlier (HOŁYŃSKI 2009) suggestion to include *Pleiona* DEYR. as a subgenus to *Cyphogastra* DEYR. was apparently an exaggeration, their close affinity seems rather firmly established.

***Pleiona tayauti* (G.-M.)**

Chrysodema tayauti GUÉRIN-MÉNEVILLE 1847: 7

Material examined:

Additional material: 14 ♂, 6 ♀, 22 ♂

Characters: Male 20×6-23×7.5, female 26×8.5-29×9 mm. Body markedly elongated, flattened, almost uniformly green with more (especially on abdomen) or less distinct golden, bronzed or cupreous hue and cupreous tips of elytra; antennae brown, tarsi dark or testaceous. Frontal depression deep, elongately triangular, reaching beyond upper margins of eyes. Pronotal sides markedly convergent; anterolateral angles poorly indicated; median sulcus narrow and shallow; laterobasal fossae somewhat c-shaped with narrow prolongation towards apical angles, extensively dfp; anteromedian foveae inconspicuous. Subhumeral protuberances poorly marked, elytral sides subparallel in anterior ²/₅, then shallowly but distinctly arcuate and very sharply, almost spiniformly denticulate, apices jointly rounded. Prosternal process narrowly but deeply medially sulcate; prometasternal ledge prominent; all abdominal segments regularly convex; anal sternite narrowly semicircularly notched (♀) or broadly triangularly emarginated (♂) at apex; sides of sternum and anterior angles of sternites extensively dfp.

Geographical distribution: In my earlier publication (HOŁYŃSKI 2009) I suggested that *P. tayauti* (G.-M.) is endemic to Hiva Oa island (Marquesas Arch.), in strict allopatry with respect to both Marquesan representatives of sg. *Guamia* THY.: *Cyphogastra* (*Guamia*) *taitina* KERR. and *C. (G.) similis* KERR.; however, later Thibault RAMAGE kindly sent me the label data of specimens in the MNHN (Paris) from Nuku Hiva, and some photographs of living beetles made *in situ*, showing that “*this species seems to be well present on that island*” (pers. inf. 13 I 2014) where it apparently co-occurs with *C. similis* KERR. (but see **Remarks** on that species!).

Bionomy: BLAIR (1935) reports 23 ♂ and 12 ♀ “*beaten from Boehmeria species*” on Hiva Oa, on Nuku Hiva it has been photographed on leaves of “*Pipturus argenteus* var. *lanosus*, 100m high, in a coconut field with *Hibiscus tiliaceus*” [det. J.-F. BUTAUD, teste T. RAMAGE (pers. inf. 14 I 2014)].



Fig. 10
Pleiona tayauti (G.-M.)



Fig. 11
Cyphogastra (Guamia) taitina KERR.



Fig. 12
Cyphogastra (Guamia) similis KERR.



Fig. 13
Cyphogastra (Guamia) longueti THY.



Fig. 14
Cyphogastra (Guamia) auripennis SND.



Fig. 15
C. (G.) auripennis v. picata KERR.

Remarks: In terms of phylogenetic affinities *Pleiona DEYR.* is evidently closely related to – a “sister”-taxon of – *Cyphogastra DEYR.* but, paradoxically, the evolution of their most characteristic morphological “diagnostic marks” proceeded in diametrically opposite directions: in contrast to “caudate” elytra (with but few – if any – minute apical denticles) and swelling (abdominal plaque) of 1. sternite, *Pleiona DEYR.* has developed swollen sternum (pro-metasternal ledge) and regularly arcuate lateroposterior elytral margins with broadly jointly rounded apices and extensive long spinose denticulation. The functional explanation of these differences is not clear to me, but they might have been originally initiated by a minor genetical modification which had “switched” them over to separate, divergent ruts.

Cyphogastra DEYR.

Cyphogastra DEYROLLE 1864: 36-37

[type-species: *Buprestis foveicollis BOISDUVAL 1835*]

Characters: Medium-sized to large (*ca.* 15-40 mm., females on the average larger than males), moderately elongated, variably coloured (from black or brown through brightly metallic cupreous, green or blue to gorgeously multicoloured; antennae and/or tarsi sometimes testaceous), variously (from very fine to coarse puncturation, with or without dfp depressions) sculptured and dorsally (except dfp areas) glabrous beetles. Frontal depression deep, triangular, not forming “mirror”, with more or less distinct deeper and coarser punctured anterior fossa; vertex rather wide. Pronotum transversely trapezoidal or tetragonal with obliquely truncated anterior angles, sulcate median line, variably shaped laterobasal fossae and more or less distinct anteromedian foveae; all these depressed areas frequently dfp. Elytra subparallelsided anteriorly, cuneate to definitely caudate in apical half, often with various longitudinal dfp sulci. Ventral side usually rather extensively dfp laterally, abdomen often with additional midlateral dfp stripes; prosternal process medially sulcate; 1. sternite swollen (maximum height of body at its apical margin), usually with more or less prominent flattened median elevation (“abdominal plaque”) at middle of apical part; apex of anal sternite rounded or narrowly notched in females, rather widely emarginate in males.

Geographical distribution: The predominantly insular distribution area extends from Java and WALLACE’s Line to French Polynesia and from Mariana Arch. to northernmost (tropical) peripheries of Australia.

Remarks: *Cyphogastra DEYR.*, probably the largest genus in the subtribe **Chrysochroina CAST.** and next to only *Psiloptera DEJ.* and *Stigmodera ESCH. (s.l.)* in the entire tribe **Buprestini LEACH**, contains *ca.* 100 known species [exact number cannot be determined because of almost completely unclarified taxonomic relationships: the last catalogue (BELLAMY 2008) is admittedly a compilation from various (often incongruent) sources and contains many separate (sometimes but remotely related) taxa listed as synonyms as well as numerous true synonyms as distinct (sub-)species]. Although the characteristic shape and sculpture of pronotum, usually strongly caudate elytra, and especially unmistakable ventral profile make *Cyphogastra DEYR.* an externally very well defined genus, as regards the internal relationships – despite the relatively large size and showy appearance of its representatives making them attractive to collectors – it is taxonomically difficult group whose modern revision is badly needed.

Key to the identification of subgenera of the genus *Cyphogastra DEYR.*

- 1 (2) Ventral profile without “fault” [fig. 3]: abdominal plaque at most slightly elevated “above” second sternite laterally but not at median line [fig. 8]) *Guamia THY.*
- 2 (1) Ventral profile with distinct “fault” [fig. 4, 5]: abdominal plaque also at middle markedly elevated “above” the 2. sternite [fig. 9] *Cyphogastra DEYR. s.str.*

***Guamia* THY.**

Guamia THÉRY 1930: 50

[type-species: *Cyphogastra auripennis* SAUNDERS 1867]

Characters: The range of body-sizes extends over that of the entire genus (*ca.* 15-40 mm., females on the average larger than males and members of the *Taitina*-circle larger than those of the *Auripennis*-circle); colour usually bright metallic (cupreous, green or blue, only in *C. latro* KERR. elytra blackish; antennae and/or tarsi usually testaceous); sculpture from very fine and sparse to rather coarse and dense, dfp areas variable on pronotum and ventral side, absent on elytra. Elytra not or but slightly caudate, sides either simply tapering to, and distinctly denticulate before, sharply spinose apices, or smooth with apices obliquely truncated and sutural denticle shorter. 1. sternite swollen (maximum height of body at its apical margin), but “abdominal plaque” indistinct or none.

Geographical distribution: The distribution strikingly disjunct: two species (*Taitina*-circle) inhabit Marquesas and perhaps (introduced?) Tahiti, three others (*Auripennis*-circle) are endemic to Mariana Arch. at the opposite side of the Pacific Ocean.

Remarks: KERREMANS (1892), describing *C. picata* KERR. – apparently the only species of this group known to him at that time (*C. picata* KERR. is a variety of earlier named *C. auripennis* SND. which, however, he seemed to have then overlooked and later misidentified) – recognized its distinctiveness [“*L’absence de la plaque abdominale et l’armature terminale de l’élytre pourraient faire constituer, pour cette espèce, une division spéciale dans le genre Cyphogastra*”], but it was only after 38 years that THÉRY (1930) drew the formal taxonomic conclusions by acknowledging the “*division spéciale*” as the subgenus *Guamia* THY. Having defined it by “*élytres terminés par une seule épine*” THÉRY (1930) explicitly excluded the Marquesan lineage [“*C. Bedoci ne pouvait rentrer dans le sous-genre Guamia*”], whose affinity to this subgenus rather than to *Cyphogastra s. str.* has been established much later (HOŁYŃSKI 1992a). *Guamia* THY. is an evidently ancient group, competitively displaced from the area of origin [what in the geological past was “Palaeomelanesia” (HOŁYŃSKI 2001b) – New Guinea, Melanesia, Samoa, &c.] by its “daughter taxon”, *Cyphogastra* DEYR. *s.str.*

Key to the identification of circles of the subgenus *Guamia* THY.

- 1 (2) Elytral magins with a series of sharp denticles before apex, sutural one long, subspinose [fig. 11, 12]. Abdominal plaque slightly but distinctly delimited laterally [fig. 8] ***Taitina*-circle**
- 2 (1) Elytral magins smooth with but single, usually short, sutural denticle [fig. 11, 12]. No abdominal plaque [fig. 8] ***Auripennis*-circle**

***Taitina*-circle**

Remarks: Marquesan branch, consisting of two species in single superspecies, characterized by incipient abdominal plaque and denticulate lateroapical margins of elytra. Pronotal sides subparallel behind anterolateral angles.

Key to the identification of species of the *Taitina*-circle

- 1 (2) Ventral side (incl. femora and tibiae) almost uniformly purplish, proepisterna at most with some green in apical angles and (narrowly) on sides [fig. 8]. Dorsal side uniformly dull-green, with oily shine, very finely (elytral disk almost imperceptibly) punctulate ***C. (G.) taitina* KERR.**

- 2 (1) Proepisterna and legs (except tarsi) predominantly green. Colouration of dorsal side brighter metallic, often with traces of oblique vittae of slightly different shade. Elytral punctulation coarser *C. (G.) similis* KERR.

***Cyphogastra (Guamia) taitina* KERR.**

Cyphogastra taitina KERREMANS 1919: 52-53

= *Cyphogastra bedoci* THÉRY v. *obscura* BLAIR 1932: 241 [nec *C. obscura* KERREMANS 1895: 202]

= *Cyphogastra obsoleta* [BLAIR i.l.] HOLYŃSKI 1992: 23-24

Material examined:

***Cyphogastra taitina* KERR.:**

Lectotype: "Coll. R. I. Sc. N. B., ILES DE LA SOCIETE | Taïti | | taitina Kerr. | Ann. Soc. Ent. Belg. 1919, 59: 52, 3 | Syntype |" "*Cyphogastra taitana*, THERY det." [♀ (KBIN)]

Paralectotypes: "*Taïti, Staud.*" "*taitina Kerr. Type*" "MUSEUM PARIS, COLL. CH. KERREMANS, 1923" [1♂, 1♀ (MNHN)]

***Cyphogastra obsoleta* HOL.:**

Holotype: "Type" "*Fatu Hiva, Marquesas, on banana, Jan 1925, St. George Expedn., C.L. Collette*" "Brit. Mus. 1925-488" "*Cyphogastra bedoci* THÉRY, det. K.G. Blair" "*Cyphogastra bedoci* Théry ab. *obsoleta* Blr. Type" [♂ (BMNH)]

Paratype: „*Fatu Hiva, Marquesas, native state: "feeds on banana", Jan. 1925, St. George Expedn., C.L. Collette*" „Brit. Mus. 1925-488" „Ex B.M.[N.H.] Duplicate" [1♀ (RBH: BPcje)]

Additional material: 26 ♂, 23 ♀, 3 ♂

Characters: Males 22×6.5-29.5×9; females 29.5×9-38×12 mm. Dorsal side rather dull-green with more or less distinct golden-bronzed reflexions and oily shine; lateral margins of elytra bright cupreous; ventral side purplish; two basal joints of antennae and distal tarsomeres brown with metallic-bronzed shine, otherwise antennae and tarsi testaceous. Dorsal side glabrous, ventral pilosity fine but rather long, erect, very sparse except in median furrow of male prosternal process and metasternum. Dorsal sculpture very fine, on elytral disk barely discernible by unaided eye; pronotal laterobasal fossae c-shaped, broad, rather extensively dfp at bottom. Anterolateral angles of pronotum well developed, tuberculate; elytra not or inappreciably caudate, margins with 5-7 sharp denticles (sutural long, subspiniform) before apex.

Geographical distribution: Despite its having been described from "*Taïti*" the species seems to naturally occur only on Fatu Hiva (southeasternmost Marquesan island): labels in old collections frequently mean the port or island from which the parcel with specimens had been sent rather than the real collecting locality; a specimen in BPBM labelled as collected on Nuku Hiva: Taiohai (northwestern group of the Archipelago) was almost certainly either mislabelled or introduced.

Bionomy: Collection labels mention either *Terminalia catappa* or bananas as [?adult] host-plants.

Remarks: The identity of *C. obscura* BLAIR (diagnosed already in BLAIR 1927, but named only five years later) and – consequently: based on the same material – *C. obsoleta* HOL. does not seem to leave any room for doubt. Differences between *C. taitina* KERR. and *C. similis* KERR. are slight and difficult to precisely describe or illustrate, but quite conspicuous in direct comparison.

***Cyphogastra (Guamia) similis* KERR.**

Cyphogastra similis KERREMANS 1919: 53
= *Cyphogastra Bang-Haasi* KERREMANS [i.l.]
= *Cyphogastra Bedoci* THÉRY 1926: 73-74
= *Cyphogastra bedoci* THÉRY v. *cyanescens* BLAIR 1932: 241-242 [issp.]

Material examined:

Cyphogastra bedoci THY.:

Holotype [not seen – *teste* T. RAMAGE *i.l.* 27 I 2014]: “I. Marquises – Bedoc” “Bedoci Théry
- Type Théry det.” “Type” [ø (MNHN)]

Cyphogastra cyanescens BLAIR:

Syntype: “[Type]” “Marquesas Is., E. Ahune, B.M. 1929-357” “*C. bedoci* Thér. ab. *cyanescens*
Blr., Type” [ø (BMNH)]

Additional material: 29 ♂, 47 ♀, 56 ø

Characters: Males 23.5×6.5-26.5×8; females 24×7.5-35.5×11 mm. Dorsal side green to bronzed; lateral margins of elytra bright cupreous; ventral side purplish melting into green anterad; antennae (except two basal joints) and basal four tarsomeres testaceous. Body practically glabrous, except very short white pubescence on dfp areas and short sparse pilosity along midline of prosternum. Dorsal sculpture fine but distinct; pronotal laterobasal fossae c-shaped, deep, more or less extensively dfp at bottom. Anterolateral angles of pronotum not prominent; elytra not or inappreciably caudate, margins with 5-7 sharp denticles (sutural long, subspiniform) before apex.

Geographical distribution: The majority of specimens of this species in collections originated from Ua Pou; I have also seen some specimens and photographs from Nuku Hiva, another island of the northern group of the Marquesan Arch., where it apparently co-occurs with *Pleiona tayauti* (*G.-M.*) – whether both of them are native there, or only one (and, in the latter case, which one?), is not quite clear for me. Highly questionable is autochthonous occurrence of *C. similis* KERR. on Tahiti, although the type-series – like in the case of *C. taitina* KERR. – and some other old specimens allegedly originated from there (as explained under the latter species, such labels not necessarily meant the actual collection locality). I have never seen (or heard of) any truly reliable record of *Cyphogastra* DEYR. from Tahiti, but recently (pers. inf. 27 II 2014) Thibault RAMAGE called my attention to the photo made in 2009 of a beetle [Moorea Biocode Specimen No. [MBIO45687](#)], apparently *C. similis* KERR. (colour rather unusual – purplish – but this may be a photographic artifact), “*captive or collected*” probably on Moorea (satellite island ca. 20 km. NW Tahiti). If the identification is correct and the beetle has really been collected on that island, the current occurrence on the Society Islands is confirmed, but even so artificial introduction seems much more likely than natural inhabitation. On some labels the locality is given as “Upolu” [second-largest island of Samoa] or “Upola”, but these are evidently misspellings of Ua Pou, so the true natural (pre-human) distribution area is almost certainly restricted to the northern group of Marquesas (Ua Pou and perhaps Nuku Hiva).

Bionomy: Unknown.

Remarks: “*C. Bang-Haasi* KERR. *i.l.*” was quoted as synonym of *C. similis* KERR. already in original description of the latter, and three “syntypes” (two examined by T. RAMAGE in MNHN and one by me in NNHM) fully confirm this conclusion; THÉRY’s (1926) detailed description of *C. bedoci* THY. also precludes any serious doubt as to its identity, while *C. cyanescens* BLAIR is but an insignificant colour aberration.

Auripennis-circle

Remarks: Western (Mariana Is.) branch – the occurrence on Caroline Is. quoted by KERREMANS (1910), repeated by OBENBERGER (1926) and discussed by BLAIR (1940) seems doubtful – includes three known species (single superspecies) without distinct abdominal plaque or lateroapical denticulation of elytra (pronotal sides convergent from basal to anterolateral angles, laterobasal fossae irregular, elongated, not dfp). Until recently the systematic relationships within this circle remained unclear to me, mainly due to almost completely unknown details of distribution: as I wrote (HOŁYŃSKI 1992a) “*C. auripennis* Saunders and *C. picata* Kerremans var. *guamensis* Kerremans have been described from Guam, and my collection contains one so labelled specimen of the Saunders’ species, but none of the remaining representatives of *C. auripennis* Saunders or *C. longueti* seen by me bears any information as to the definite locality within the archipelago”; however, KUROSAWA’s (1953) publication (unknown to me until mid-1990-s) and later examined specimens from the collections of BPBM, CLB, MNHN, NNHM and USNM have largely clarified both the geographical and – consequently – taxonomical situation.

Key to the identification of species of the *Auripennis*-circle

- 1 (4) Elytra green to cupreous-red [fig. 13, 14, 15]
- 2 (3) Elytra green with contrasting cupreous lateroapical band [fig. 13], anal sternite testaceous, tarsi dark. Punctulation of dorsal side very fine *C. (G.) longueti* THY.
- 3 (2) Elytra cupreous-red with small periscutellar area [fig. 14] or more or less extensive anteromedian parts of disk [fig. 15] green, anal sternite metallic, 1.-4. tarsomeres testaceous. Elytral punctulation coarser *C. (G.) auripennis* SND.
- 4 (1) Elytra brownish-black [fig. 16] *C. (G.) latro* KERR.

Cyphogastra (Guamia) longueti THY.

Cyphogastra auripennis ssp. *Longueti* THÉRY 1926: 63

= *Cyphogastra auripennis* SAUND. sensu KERREMANS 1910: 171-172

Material examined:

Additional material: 8 ♂, 14 ♀, 3 ♂

Characters: Males 17×5-19×6; females 23×7-28×9 mm. Bright green with contrasting cupreous-red (graduating through golden middle to green basal half) lateroapical elytral band and testaceous anal sternite; antennae and tarsi dark reddish-brown. Dorsal side glabrous, short ventral pubescence restricted to dfp areas and furrow along prosternal process. Dorsal sculpture very fine. Anterolateral angles of pronotum well developed, tuberculate; elytra slightly caudate, apices strongly obliquely truncated, smooth except long sutural denticle.

Geographical distribution: *C. longueti* THY. inhabits Saipan, the northernmost of the four large islands making the main group of the Mariana Archipelago. The specimen of “*C. auripennis* SND.” from Caroline Is. in THÉRY’s collection, mentioned by KERREMANS’ (1910), might have belonged to this species (see **Remarks** below), but was anyway probably mislabelled.

Bionomy: Four specimens in the USNM are labelled as collected on *Terminalia* (two of them concretely on *T. catappa*).

Remarks: KERREMANS (1910) misinterpreted SAUNDERS’ (1867) description and applied the name *C. auripennis* SND. to what has later been named *C. longueti* THY. THÉRY (1926) discovered the mistake and described the latter as a subspecies of *C. auripennis* SND.,

considering it synonymous with *picata* KERR. and *guamensis* “MEY. DARC. mss.” (it is unclear why, then, he decided to create a new name?) both of which, however, belong to the true *C. auripennis* SND. [this was realized already by KERREMANS (1911) who thus, paradoxically, by removing them from *C. auripennis* SND. (sensu KERREMANS) put them in synonymy of... *C. auripennis* SND. (sensu SAUNDERS)!].

***Cyphogastra (Guamia) auripennis* SND.**

Cyphogastra auripennis SAUNDERS 1867: 432-433

= *Cyphogastra picata* KERREMANS 1892: 23-24

= *Cyphogastra guamensis* [MEYER-DARCIS i.l.] KERREMANS 1911: 294 [?unavailable]

Material examined:

***Cyphogastra auripennis* SND.:**

Holotype: „Type” „Guam” „*auripennis* ES” „Saunders 74.18” [ø (BMNH)]

***Cyphogastra picata* KERR.:**

Syntypes: „Type?” „Mariannes, Baer” „*picata* Kerr., Type” „Kerremans 1903-59” [1 ♀ (BMNH)]; “Coll. R. I. Sc. N. B., Iles Carolines | Mariannes | Marche | ex coll. A. v. Hoscheck” “*picata* Kerr. 1892, cf. Ann. Soc. ent. Fr. 1892, 61: 23, 4 | Syntype |” “*auripennis picata* Kerr., det. Hoscheck 192.” [1 ♀ (KBIN)]; “1607” “Coll. R. I. Sc. N. B., Iles Carolines | Mariannes | A. Marche | ex coll. A. v. Hoscheck” “*picata* Kerr. 1892, cf. Ann. Soc. ent. Fr. 1892, 61: 23, 4 | Syntype |” [1 ♀ (KBIN)]

***Cyphogastra guamensis* M.-D.:**

?Syntypes: „Guam, 17.X.94” „*Cyphogastra guamensis* Kerr.” „Type” „MUSÉUM PARIS, 1952, COLL. R. OBERTHUR” „TYPE” [red label] [1 ♀ (MNHN)]; „Guam, 20.X.94” „Type” „type” „Museum Leiden, Ex coll. G. van Roon” [1 ♀ (NNHM)]

Additional material: 6 ♂, 12 ♀, 1 ø

Characters: Males 17.5×5.5-21.5×7; females 23.5×7-28×9 mm. Head, thorax and 1. sternite green, rest of abdomen cupreous, elytra cupreous with more or less extensive mid-discal (v. *picata* KERR.) or only small periscutellar (*f.typ.*) area green, antennae piceous-brown, tarsi testaceous except brown 5. joint. Body glabrous, only ventral dfp areas and furrow along prosternal process covered with very short white pubescence. Median areas of ventral side practically impunctate, otherwise sculpture fine but distinct. Anterolateral angles of pronotum poorly marked; elytra slightly caudate, apices obliquely truncated, smooth except short sutural denticle.

Geographical distribution: *C. auripennis* SND. seems endemic of Guam, the largest and southernmost of Mariana Is. Records from Caroline Is. (KERREMANS 1910, OBENBERGER 1926) had probably resulted from misinterpretation: see e.g. the labels of the KBIN syntypes of *C. picata* KERR., possibly those referred to by KERREMANS 1910 as “*îles Carolines (coll. Théry)*”.

Bionomy: one specimen in BPBM has – according to the label – been collected on *Antigonum*, eight in USNM on *Terminalia catappa*.

Remarks: The “types” in MNHN and NNHM might have been intended as syntypes of *C. guamensis* MEYER-DARCIS but **not** as *C. guamensis* KERREMANS: KERREMANS (1911) considered this “*amplification des caractères du C. picata*” a simple colour variety “*qui ne peut en être séparée*”, and did not quote any “type” material, having evidently no intention to “validate” the name; however, as it has nevertheless been generally accepted as nomenclaturally available and cited as a synonym (BELLAMY 2008) or variety (OBENBERGER 1926), the quotation of MEYER-DARCIS’ “syntypes” seems warranted.

***Cyphogastra (Guamia) latro* KERR.**

Cyphogastra latro KERREMANS 1910: 173-174

Material examined:

Cyphogastra latro **SND.:**

Lectotype: „MUSEUM PARIS, MARIANNES, A. MARCHE 1888” „990 88” “TYPE” [red letters] „*Cyphogastra latro* Kerrem., Type” [♂ (MNHN)]

Paralectotype: “Paratype” „Museum Paris, Mariannes, A. Marche 1888” „990 88” „*Cyphogastra latro* Kerr., PARATYPE” „1937.373” [♀ (BMNH)] **or** „*Iles Mariannes, A. Marche 1888*” „*latro* Kerrem., Type” “Cotype” [red label] „*Cyphogastra latro* Kerr., cotype, A. Descarpentries det.” [♀ (MNHN)]

Additional material: 2 ♂, 3 ♀

Characters: Males 19×6-19.5×6; females 20.5×6-27.5×9 mm. Elytra brownish-black, otherwise body cupreous with some green on sides of ventral surface; antennae piceous-brown, basal four tarsomeres testaceous. Dorsal side glabrous, white ventral pubescence short but abundant, dense on lateral dfp areas and (especially in male) in median furrow of prosternal process. Sculpture relatively coarse. Anterolateral angles of pronotum well marked but not protruding; elytra slightly caudate, apices strongly obliquely truncated, smooth except long sutural denticle.

Geographical distribution: *C. latro* KERR. seems endemic to Rota, the central (at *ca.* midway between Guam on the southwest and Tinian-Saipan group on the northeast) of the large islands of the Mariana archipelago.

Bionomy: Three specimens in the USNM have been collected on *T. catappa*.

Remarks: *Cyphogastra latro* KERR. has been described from "*Iles Mariannes (Muséum de Paris, par A. Marche: 2 exemplaires)*" (1 male and 1 female) of "*Long. 20-25; larg. 6-8 millim.*". Notes from my visit in BMNH (1978) contain the label data of a female specimen [“Paratype” „Museum Paris, Mariannes, A. Marche 1888” „990 88” „*Cyphogastra latro* Kerr., PARATYPE” „1937.373”] seemingly in full agreement with the details of original description, and until recently I considered it as one of the two syntypes (KERREMANS had not designated a holotype). However, having visited the Paris Museum few years ago, I found there and borrowed for study two other specimens labelled as types [„MUSEUM PARIS, MARIANNES, A. MARCHE 1888” „990·88” “TYPE” [red letters] „*Cyphogastra latro* Kerrem., Type” (♂: 19.5×6 mm.); and „*Iles Mariannes, A. Marche 1888*” „*latro* Kerrem., Type” “Cotype” [red label] „*Cyphogastra latro* Kerr., cotype, A. Descarpentries det.” (♀: 25×7.5 mm.)]. Except for “TYPE” vs. “PARATYPE” the labels of the male in Paris seem to agree in every detail (up to the round “990·88”) with the female examined in London, but those of Paris female also match the data of the description, and measurements of both Paris specimens fit these data as well. So, we have three reasonable candidates for types, although only two of them can be “available” – which two? both from Paris? or the two (Paris male and London female) with near-identical labels? Anyway, it seems logical to designate as lectotype the Paris male, as it appears in both possible combinations (and I have it before me), but it remains unclear which female is the true paralectotype – perhaps the measurements of the London specimen can provide the negative (if significantly differ from 25×8 mm.) evidence?



Fig. 16
Cyphogastra (Guamia) latro KERR.



Fig. 17
Cyphogastra (s.str.) tinianica KUR.

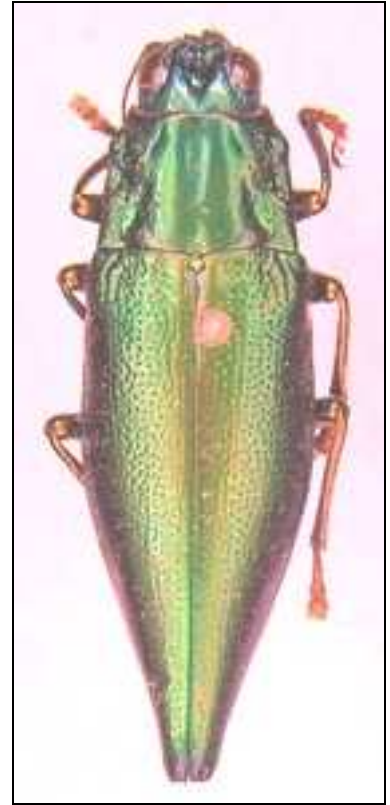


Fig. 18
C. (s.str.) uxorismeae HOL.



Fig. 19
Cyphogastra (s.str.) wallacei DEYR.



Fig. 20
Cyphogastra (s.str.) satrapa (SCHH.)



Fig. 21
Metataenia (Chalcomr.) coelestis KERR.

Phylogenetical reconstruction

The unusual distribution of *Guamia THY.* – two circles, each inhabiting another of the two groups of relatively small islands separated by 9000 km. of ocean, but absent from any intermediate archipelago where, in turn, many species of the nominotypical subgenus abound – makes the question of its phylogenetic history extraordinarily interesting, while the presence on Marianas of morphologically and geographically enigmatic *C. tinianica KUR.* and on Marquesas of no less mysterious *Pleiona DEYR.* add further intriguing question-marks.

As usual, my phylogenetic reconstruction has been performed with MICSEQ – the general outline of the algorithm with presentation and justification of basic assumptions, as described by HOŁYŃSKI (2001a, 2009), remains valid, albeit the program has been since largely computerized, some details of procedure modified, and some errors eliminated. I am seriously skeptical as regards the real value of “exact” statistical tests (bootstrap, jackknife, Bayesian posterior probability, &c.) designed to evaluate the support for particular branches of cladograms – in my opinion they are simply misleading (“*their application gives a stamp of extreme exactitude and reliability to conclusions even if derived from faulty, though sufficiently numerous, data*” – UVAROV 1931, *teste* KRELL 2004): statistics is an effective tool in eliminating **random, stochastic** inexactitudes, but is powerless against **systematic** errors [non-representative taxon- od character-sampling, false homology (“alignment” in molecular analyses), inadequate weighting, suboptimal “model”, inappropriate method, &c.] dominating in reconstructions of phylogeny and overwhelmingly influencing the results. Moreover, in the tests evaluating entire tree at once, the estimated likelihood of any clade is dependent of all the others, what further decreases its reliability. Therefore, in my reconstructions, I do not make any attempt to “chase a phantom” of exactitude, preferring to approximately evaluate the plausibility of each node separately “by eye”, assisted only by “support quotient” **SQ=x/y** (in phenuns) [where **x** is the “corrected distance” (at the relevant stage of analysis, *i.e.* when the particular pairing is being performed) between the paired taxa, and **y** – the shortest distance between any of them and any of those remaining “in game”; **phenun (pu)** is a unit of the “cost of transformation” between character states, *i.e.* of phenetic distance between analysed taxa: **1 pu** = distance between two neighbour traits in the transformation chain if the weight has been settled as 1 (HOŁYŃSKI 2005)].

“*Chalcotaenia 6Y*” and “*Metataenia 6U*” – the ancestors of the respective taxa as reconstructed in HOŁYŃSKI (2009) [cladogram 6 (: 388) and the respective character-matrix (: 375-376)] – served only as out-groups; similarly, *C. uxorismeae HOL.*, *C. wallacei DEYR.* and *C. satrapa (SCHH.)* have been included merely to clarify the phylogenetical affinities (closer to *Guamia THY.* or to *Cyphogastra DEYR. s.str.?*) of *C. tinianica KUR.*, their specific (not directly relevant to *Guamia THY.* or *C. tinianica KUR.*) characters were not sampled for character-matrix, so the internal relationships within the “clades” **[X]** and **[F]**, as not interpretable, have not been (and should not be) analyzed.

According to the so performed analysis [Fig. 22], the ancestral “proto-*Cyphogastra*” **[I]** appears as a dorsally uniformly (no contrasting lateral band on elytra) green beetle with cupreous abdomen, pale (testaceous) antennae and proximal 4 tarsomeres; subparallelsided pronotum of no or inconspicuous collar and anterolateral angles; shallow median furrow, and laterobasal fossae in form of longitudinal, slightly dfp sulci; narrow and finely punctulated laterobasal reliefs and entire lateral carina; elytra slightly caudate, lateroapical margins multidentulate, apices markedly oblique with prominent sutural denticle; elytral sculpture fine with no dfp pattern; basal sternite not sulcate, abdominal plaque discernible but slight, midlateral dfp stripes at least on anal sternite distinct, otherwise abdominal punctulation very

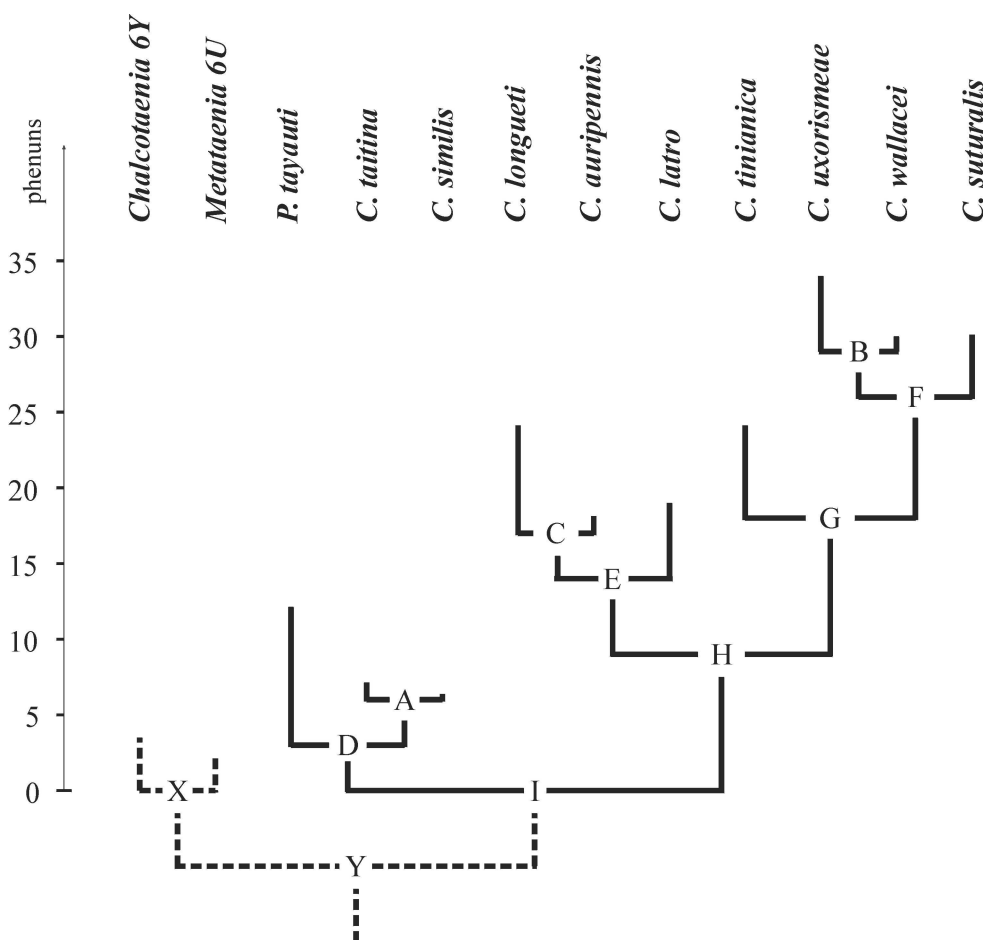


Fig. 22
Phylogenetical relations between basal branches of the *Cyphogastra*-supergenus

sparse with no conspicuous lateral dfp depressions – a character complex placing it evidently not only in the subgenus *Guamia* THY., but concretely in the *Taitina*-circle!

All the closest relatives of the *Cyphogastra*-supergenus live in or around the area for which I (HOLYŃSKI 2001b) coined the term “Palaeomelanesia”: according to the present knowledge there have never been extensive subaerial areas – to say nothing of GRESSITT’s (1958) “*Melanesian continent*” – to the East of Australia but, throughout the Cenozoic, island chains (of changing configuration and extremely complicated history) extended from what is now Central Range of New Guinea through New Caledonia to New Zealand (“Inner Melanesian Arc” – the leading edge of the Australian plate after breakage of Gondwana) and from the present northern New Guinea, Bismarck Archipelago, Solomons and New Hebrides to Fiji and Tonga (“Outer Melanesian Arc” of oceanic derivation) (YAN & KROENKE 1993, COLEMAN 1997, HALL 2002). The arcs and their parts moved thousands of kilometers, individual islands emerged and submerged; their area, elevation, distance from continent and from one another incessantly changed; some have become accreted to larger land-masses (mainly to New Guinea) or drifted as far apart as Moluccas and Philippines – all this promoted intensification of evolutionary processes (dispersal, transspeciation, diversification) making Palaeomelanesia an important center of origin and radiation of several groups of organisms (*cf. e.g.* BOER & DUFFELS 1996), among others the **Paracuptoid lineage** of the **Buprestidae** LEACH (HOLYŃSKI 1997, 2009). Thus, the “proto-*Cyphogastra*” evidently evolved somewhere in that fascinating region, and probably there dissipated [*cf.* HOLYŃSKI (2009) for the term] into (probably southeastern) [D] and (northwestern) [H].

Almost (except for the appearance of cupreous lateroposterior band on elytra and more extensive dfp bottoms of laterobasal pronotal fossae) unchanged [D] had, before having apparently been overcompeted by [descendants of?] its “sister” in Palaeomelanesia, successfully colonized remote Marquesan archipelago. How it managed to do so is one of the mysteries of the early evolution of the group: BLAIR’s (1927) remark that the “*presence of the genus Cyphogastra, not unsupported by other evidence, is suggestive of a Papuan origin, by way of New Hebrides, Fiji, etc.*” represents the most obvious hypothesis of “stepping stone” dispersal over the archipelagoes between 10⁰ and 20⁰S. This seemed indeed a reasonable assumption in the context of the recent topology: between New Guinea and New Hebrides the chain of large islands is rather dense, and even several hundred km. distance from there to Fiji and then to Tonga might not appear as an unsurmountable barrier; further east, up to the French Polynesia, islands appropriate for “stepping stones” (low coral atolls are evidently *not* appropriate) are very sparse, separated from one another by thousands of kilometers – rather too much even for so strong flyers as large buprestids (to say nothing of the probability of hitting a tiny islet in the boundlessness of ocean...), but anyway Tonga Archipelago reduces the distance to Marquesas by half (*ca.* 3800 *vs.* 7600 km.) as compared to that from New Guinea.

Another conceivable mechanism would be to “ride” (non-stop) a tree floated by appropriate current. Ocean currents at low latitudes run predominantly westwards, but the Equatorial Counter Current is the exception. On most maps it is depicted as a single “stream” somewhat north of Equator, but also “*an eastward-flowing current of speeds from 10 to 25 cm./sec. is indicated ... in the Pacific Ocean south of the equator in a position roughly symmetrical to that of the (North) Equatorial Countercurrent ... between lat. 2° S. and 5° S. at long. 165° E. and progressively farther south toward the east, to between lat. 10° S. and 14° S. at long. 95° W*” (REID 1959). Starting point would be somewhere near the modern Solomon Is. [fig. 23], the distance to Marquesas would be longer (at least *ca.* 7000 km.), and the “raft” would need no less than 10 months but probably more than a year to reach there – could a beetle have survived such a voyage? An adult sitting on the bark, spattered with seawater and slashed with wind, would certainly die within a day or two, but for larvae, anyway long-lived and, deep in the wood, rather efficiently protected against adverse environmental vagaries, a year long travel seems well within the realm of capabilities – at least if the wood itself remains in tolerable condition. Host-plants of the representatives of sg. *Guamia* THY. are not known (at least to me) for sure, but all species for which any bionomic data exist have been collected on *Terminalia* (usually *T. catappa*), a tree widely distributed throughout southern Pacific archipelagoes and renowned for its resistance to water, what seems to make survival conceivable and passive “rafting” perhaps more likely than active “island hopping”.

Whatever might have been the route, anyway [D] managed to invade Marquesas. The chronology of this invasion is not known, but the amount of morphological differentiation between the descendants of [D] shows that it must have occurred rather long ago; the palaeogeographic maps of HALL (2002) allow to hypothesize that it might have occurred towards the end of Oligocene (some 30-25 million years ago), before breaking of the most convenient “bridge” (probable chain of “stepping stones”) between Palaeomelanesia and Mariana Is. – perhaps the most likely way of later expansion of the *Auripennis*-circle and *C. tinianica* KUR. to their current homeland. The oceanic plateau underlying Marquesas seems to be much older (34-43 m.y. – GUTSCHER & *al.* 1999) than any of the relatively recent – from 1.3 (southernmost Fatu Hiva) to 6 (northwesternmost Eiau) million years – presently subaerial islands. Anyway the oldest is, and evidently has always been, the – closest to Palaeomelanesia – NW part of the archipelago, and some (now non-existent) island of that part was the most

likely landing point of the newcomer [D] and first bridgehead of its spreading and further evolving population.

The astoundingly asymmetrical first branching here [fig 24] – between almost unchanged [A] (only cupreous sternum and subparallel pronotal sides distinguished it from [D]) and the ancestor of drastically different (dark tarsi, jointly rounded not caudate elytra, practically absent midlateral dfp stripes of abdomen, but especially prometasternal ledge instead of abdominal plaque, supplemented with some autapomorphies – strongly flattened body, unusually long and sharp elytral denticulation, &c. – not considered in the phylogenetic analysis) *Pleiona DEYR.* – is another mystery of the early stage of [*Cyphogastra DEYR.*]-super-genus evolution. As a partial explanation we could suppose that it was the “proto-*Pleiona*” that colonized further island[-s] of the archipelago and perhaps changed the host-plant[-s] [true larval hosts remain unknown, but although all species of *Guamia THY.* seem associated with *Terminalia* (**Myrtales: Combretaceae**), *Pleiona tayauti G.-M.* was collected/photographed on completely unrelated *Boehmeria* or *Pipturus* (**Rosales: Urticaceae**)], whereas [A] behaved in both respects conservatively (it is tempting to speculate that *Terminalia* arrived to Marquesas not much before [D] and was not yet widely distributed there; if so, the conversion of *Pleiona DEYR.* to **Urticaceae** might have been constrained by lack of the original host-plant on the newly colonized island). The further differentiation of [A] seems to have consisted only of relatively recent dispersal to Fatu Hiva and development of still finer punctulation in the resulting *C. taitina KERR.*, while the “mother” population has apparently remained unchanged and now inhabits Ua Pou (and perhaps Nuku Hiva) as *C. similis KERR.*

Meanwhile the northwestern populations of [I], occupying perhaps the islands of the South Caroline Arc, underwent several slight modifications (antennae became yellow, collar, anterolateral angles and median furrow on pronotum more strongly accentuated, laterobasal reliefs robust and more coarsely punctured, lateroapical denticulation except sutural denticle of elytra disappeared) to become [H] and later expand by “island hopping” along Mariana Ridge [fig. 25], where it evolved into the ancestor of the *Auripennis*-circle ([E]) of greenish-bronzed pronotum, cupreous elytra, again poorly marked anterolateral pronotal angles, laterobasal fossae not dfp, and no trace of abdominal plaque. The first split of [E]) might have occurred between the population which stopped expansion on the southernmost island of the archipelago, Guam (whose evolution into [C] involved only colouration: reversal of head and pronotum into green and development of cupreous lateral band on elytra) and more “adventurous” group tending further north, to Rota I., where it became the dark-bodied, rather coarsely sculptured *C. latro KERR.* with extensively dfp sides of abdomen. Having later sent another troop of conquerors still further north, to Saipan (*C. longueti THY.* of elytral colouration reversed to green, abdomen also green with testaceous anal sternite, dark brown tarsi and very fine sculpture) the beetles on Guam (*C. auripennis SND.*) remained practically unchanged: only sutural denticle of elytral apex became less prominent.

Southern populations of [H] evolved *in situ* into [G] (the ancestor of the sg. *Cyphogastra DEYR. s.str.*: elytral disk cupreous, pronotum subparallelsided, elytra definitely caudate with narrowly transversely truncated apices and minute sutural denticle, prominent abdominal plaque) which, after having sent an outpost (recent *C. tinianica KUR.* – dorsal side bronzed, male anal sternite non-metallic ferruginous, tarsi yellow, protruding anterolateral pronotal angles) to follow the traces of the *Auripennis*-circle and colonize the remote Tinian I. (northern Marianas), spread to the south (modern New Guinea) to become (by reversal of elytral colouration to green, change of that of abdomen also to green and of tarsi to dark brown, secondary loss of lateroapical elytral denticulation except sutural denticle, coarser

dorsal and denser ventral sculpture) the ancestor ([F] of all the remaining species of *Cyphogastra* DEYR.

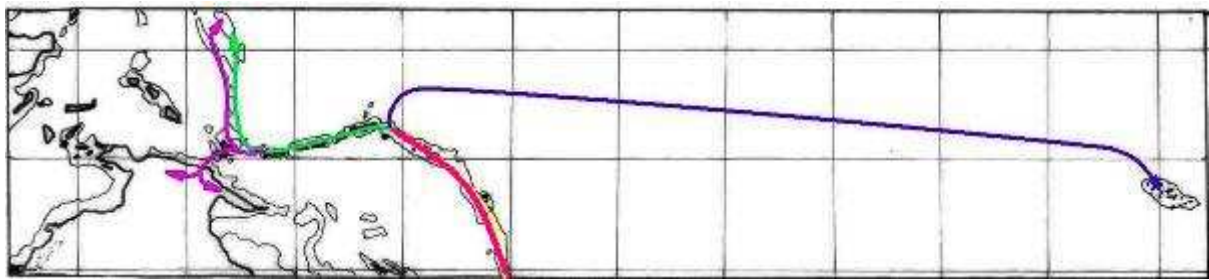


Fig. 23

Early dispersal of the *Cyphogastra*-super-genus

Red – ancestor; blue – Marquesan lineage; green – [*Auripennis*]-superspecies; purple – *Cyphogastra* s.str.
[Late Oligocene topography of equatorial Pacific based mainly on HALL (2002) and GUTSCHER & al. (1999)]



Fig. 24

Geocladograms

Marquesan branch of *Cyphogastra*-super-genus

- – *Pleiona* DEYR. ; ● – *C. (G.) similis* KERR.;
- – *C. (G.) taitina* KERR.



Fig. 25

Mariana branches of *Cyphogastra* DEYR.

- – *C. (G.) auripennis* SND.; ● – *C. (G.) latro* KERR.;
- – *C. (G.) longueti* THY.; ● – *C. tinianica* KUR.

The “double invasion” of Marianas, with *C. tinianica* KUR. having apparently “leap-frogged” the earlier invaders (*C. auripennis* SND. on Guam and *C. latro* KERR. on Rota I.) to colonize one of two northernmost large islands of the archipelago, is yet another mysterious feature of *Cyphogastra* DEYR. evolution: the fact that the only two successful invasions of Mariana Is. by that speciose genus were accomplished just by two successive basal branches, and that the later invader occupies an island between those inhabited by descendants of the earlier one (and, at that, near to the northernmost end of the chain!), is not easy to interpret.

The most likely (or, maybe, only the least unlikely...) seems the “scenario” based on geotectonic history of the area: in mid-Oligocene what is now represented by the Palau-Kyushu and Mariana Ridges was a single linear structure whose southern end almost touched the NW end of the Outer Melanesian Arc (HALL 2002), offering the best opportunity for the ancestor of the *Auripennis*-circle to disperse northwards; later the northern half of that primaeval elevation started to split longitudinally, with eastern part – the incipient Mariana Ridge – drove progressively away, but the separation advanced from south to north so that up to the Early Miocene the northern sections of the “daughter”-ridges remained close to one another, leaving also the meanwhile evolved proto-*Cyphogastra* DEYR. *s.str.* a possibility to invade (northern!) Marianas and there develop into *C. tinianica* KUR.

Acknowledgements

I am greatly indebted to all those – by far too numerous to be listed here... – who offered me material, help and advice in my four decades long studies on the Indo-Pacific faunae in general and *Cyphogastra* DEYR. in particular: without them I would never be able even to start planning a project like this. My special thanks are due to Thibault RAMAGE, who kindly sent me so many valuable informations, data and pictures elucidating several problems concerning the Marquesan branch of the *Cyphogastra*-supergen.

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Appendix

Character definitions

Upper line – codes of traits [“character-states”]; ***[bold italics]*** – terminals of a transformation chain

Lower line – weights (costs of transformation) [0↔1↔2=1: additively equidistant (distance between 0 and 1 the same (=1) as between 1 to 2, that between 0 and 2 = 1+1 = 2)]

Colour

1. Head and pronotum: ***[0]*** green; ***[1]*** greenish-bronzed; ***[2]*** cupreous
0↔1↔2=1
2. Elytra (disk): ***[0]*** green; ***[1]*** cupreous; ***[2]*** bronzed; ***[3]*** black
0↔1↔2↔3=1
3. Elytra (postero-lateral band): ***[0]*** cupreous; ***[1]*** concolorous
0↔1=2
4. Sternum: ***[0]*** green; ***[1]*** cupreous
0↔1=1
5. Abdomen (1.-4. sternites): ***[0]*** green; ***[1]*** cupreous or blackish
0↔1=1
6. Abdomen (anal sternite): ***[0]*** metallic; ***[1]*** ferruginous in male; ***[2]*** yellow in both sexes
0↔1↔2=1
7. Antennae: ***[0]*** dark brown; ***[1]*** yellow
0↔1=2
8. Tarsi: ***[0]*** dark brown; ***[1]*** 1.-4. joints yellow, claw joint dark; ***[2]*** only claws dark
0↔1=2; 1↔2=1

Pronotum

9. Side margins: ***[0]*** subparallel; ***[1]*** distinctly convergent
0↔1=2
10. Collar: ***[0]*** none or inappreciable; ***[1]*** distinct
0↔1=1
11. Anterolateral angles: ***[0]*** not prominent; ***[1]*** slightly tuberculate; ***[2]*** projecting outwards
0↔1=1; 1↔2=2
12. Median furrow: ***[0]*** shallow; ***[1]*** deep
0↔1=2
13. Lateral depressions: ***[0]*** longitudinal sulci; ***[1]*** broad fossae
0↔1=2
14. Lateral depressions: ***[0]*** not dfp; ***[1]*** slightly dfp; ***[2]*** extensively dfp
0↔1↔2=1
15. Laterobasal reliefs: ***[0]*** robust, coarsely punctured; ***[1]*** narrow, finely punctulated
0↔1=1
16. Lateral carina: ***[0]*** to apical third; ***[1]*** entire
0↔1=1

Elytra

17. Shape: ***[0]*** not caudate; ***[1]*** slightly caudate; ***[2]*** strongly caudate
0↔1=1; 1↔2=2
 18. Lateroapical margins: ***[0]*** multidenticulate; ***[1]*** smooth except sutural denticle
0↔1=2
 19. Apices: ***[0]*** jointly rounded; ***[1]*** markedly oblique; ***[2]*** transversely truncate
0↔1↔2=1
 20. Sutural denticle: ***[0]*** minute; ***[1]*** prominent
0↔1=1
 21. Elytral dfp pattern: ***[0]*** none; ***[1]*** prominent
0↔1=3
 22. Sculpture: ***[0]*** very fine; ***[1]*** moderately fine; ***[2]*** relatively coarse
0↔1↔2=1
- #### Ventral side
23. Prometasternal ledge: ***[0]*** none; ***[1]*** prominent
0↔1=3
 24. Abdominal plaque: ***[0]*** none; ***[1]*** slight; ***[2]*** prominent
0↔1=1; 1↔2=2
 25. Basal sternite: ***[0]*** convex; ***[1]*** sulcate
0↔1=2
 26. Midlateral dfp stripes on abdomen: ***[0]*** none or inconspicuous; ***[1]*** distinct at least on anal sternite
0↔1=1
 27. Lateral dfp depressions on abdomen: ***[0]*** none or inconspicuous; ***[1]*** extensive; ***[2]*** entire sides
0↔1↔2=1
 28. Abdominal punctures: ***[0]*** moderately sparse; ***[1]*** very sparse
0↔1=1

Character matrix

red italics: apomorphies; pink italics underlined: reversals; below the red line --- : outgroups (not analysed)
second row: cost of direct transformation between 0 and x; third row: cost of transformation 1↔2 (if different)
last two columns: =distance from last ancestor [Support Quotients]

	12345	67890	12345	67890	12345	678	
	11211	12221	12211	11211	31312	111	
		1	2	2	2		
<i>P. tayauti</i>	00001	01010	00021	10001	01100	011	=9
<i>C. taitina</i>	00011	01100	00021	11011	00010	101	=1
<i>C. similis</i>	00011	01100	00021	11011	01010	101	=0
<i>C. longueti</i>	0000	20011	01000	11111	00000	101	=7
<i>C. auripennis</i>	01001	00111	01000	11110	01000	101	=1
<i>C. latro</i>	23101	00111	01000	11111	02000	110	=5
<i>C. tinianica</i>	12101	10201	21010	12120	01020	101	=6
<i>C. uxorismeae</i>	00111	00111	11000	12020	02020	000	=5
<i>C. wallacei</i>	00100	00011	01000	12020	02020	100	=1
<i>C. satrapa</i>	00000	00001	11010	11020	02020	110	=4
A	00011	01100	00021	11011	01010	101	=3 [1/ 8]
B	00100	00011	11000	12020	02020	100	=3 [6/ 9]
C	01001	00111	01000	11111	01000	101	=3 [6/ 8]
D	00001	01110	00021	11011	01010	101	=3 [8/16]
E	11101	00111	01000	11111	01000	101	=5 [8/14]
F	00100	00001	11010	12020	02020	100	=8 [9/14]
G	01101	00101	11010	12120	01020	101	=9 [10/13]
H	00101	00111	11010	11111	01010	101	=9 [6/11]
I	00101	01110	00011	11011	01010	101	=4 [2/12]
<i>Metataenia 6U</i>	02111	01110	00121	01010	12001	021	=2
<i>Chalcotaenia 6Y</i>	12100	01110	11121	01010	11001	021	=3
X	02101	01110	00121	01010	11001	021	=2 [7/18]
			1				
Y	01101	01110	00021	11011	01000	111	
			11	0	0	1	1
				0	1	1	0