

# Morphology and phylogenetic analysis of five deep-sea golden gorgonians (Cnidaria, Octocorallia, Chrysogorgiidae) in the Western Pacific Ocean, with the description of a new species

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## Abstract

Explorations of seamounts in the Western Pacific Ocean and South China Sea resulted in collecting 18 specimens of golden gorgonians. Based on the morphology and the genetic analysis of mtMutS, they are described as one new species, *Chrysogorgia carolinensis* **sp. nov.**, and four known species, including *Chrysogorgia dendritica* Xu, Zhan & Xu, 2020, *Metallogorgia melanotrichos* (Wright & Studer, 1889), *Metallogorgia macrospina* Kükenthal, 1919, and *Pseudochrysogorgia bellona* Pante & France, 2010. *Chrysogorgia carolinensis* belongs to the *Chrysogorgia* “group A, Spiculosae” with rods or spindles distributed in the polyp-body wall and tentacles, and differs from all of its congeners except *C. dendritica* by the 1/3L branching sequence and amoeba-shaped sclerites at the basal polyp body. The mtMutS sequence of *C. carolinensis* **sp. nov.** has six deletion mutations compared to those of its congeners, supporting the establishment of the new species. Although no genetic variability was observed between the closely related species *C. dendritica* and *C. abludo* Pante & Watling, 2012, the former is different from the latter by the apparently irregular sclerites in the polyp body wall. The two specimens of *Metallogorgia melanotrichos* match well with the original description except for relatively larger polyps, while the *M. macrospina* specimens have slightly

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smaller polyps than the holotype. The juvenile of *Metallogorgia* has an obvious morphological difference with the adults in the colony shape and branches, but they can be unified by the same polyps and sclerites as well as mitochondrial MutS sequences. Thus, the generic diagnosis of *Metallogorgia* is slightly extended to include the morphology of juveniles. The morphology of *Pseudochrysogorgia bellona* Pante & France, 2010, as a new record for the South China Sea, matches well with that of the original description. In the phylogenetic trees, the *Chrysogorgia* species are separated into two clades, and while *Metallogorgia* and *Pseudochrysogorgia* formed a sister clade.

### Keywords

Anthozoa, *Chrysogorgia dendritica*, *Chrysogorgia carolinensis*, *Metallogorgia*, *Pseudochrysogorgia*, seamount

## Introduction

Chrysogorgiids are found in all major oceans from Iceland to Antarctica, and they are conspicuous members of deep-water benthic assemblages (Pante et al. 2012). The family Chrysogorgiidae Verrill, 1883 currently contains 14 genera, with 12 genera having been analyzed by molecular phylogenetic methods with and six of them forming a monophyletic clade (called the Monophyletic Chrysogorgiidae Clade, or MCC), including *Chrysogorgia* Duchassaing & Michelotti, 1864, *Pseudochrysogorgia* Pante & France, 2010, *Iridogorgia* Verrill, 1883, *Rhodaniridogorgia* Watling, 2007, *Radicipes* Stearns, 1883 and *Metallogorgia* Versluys, 1902 (Watling et al. 2011; Pante et al. 2012).

The genus *Chrysogorgia* Duchassaing & Michelotti, 1864 contains 75 species and is distributed worldwide (Watling et al. 2011; Cairns 2018; Xu et al. 2020). It is characterized by four branching forms of the colony, including a single ascending spiral (clockwise or counterclockwise, bottlebrush-shaped colony), a single fan (planar colony), two or more fans emerging from a short main stem (bi- or multi-flabellate colony) and a bush of branches perched on top of a long straight stem (tree-shaped colony) (Pante and Watling 2012; Cordeiro et al. 2015; Xu et al. 2020). Based on the shapes of rods or scales in the polyp-body wall and tentacles, four groups have been recognized for the separation of *Chrysogorgia* species, including “group A, Spiculosae” with 42 species, “group B, Squamosae aberrantes” with 13 species, “group C, Squamosae typicae” with 19 species and “group D, Spiculosae aberrantes” with only one species (Versluys 1902; Cairns 2001; Cordeiro, Castro and Pérez 2015; Xu et al. 2019).

The genus *Metallogorgia* Versluys, 1902 is distinguished from *Chrysogorgia* by its distinctive monopodial stem with branchlets forming a sympodium pattern in strong branches, sclerites with no distinction in coenenchyme or polyps, and coenenchyme thin with few sclerites (Versluys 1902). The establishment of *Metallogorgia* was well supported by a phylogenetic analysis (Pante et al. 2012). At present, there are four species in this genus: *M. melanotrichos* (Wright & Studer, 1889), *M. macrospina* Kükenthal, 1919, *M. splendens* (Verrill, 1883) and *M. tenuis* Pasternak, 1981 (Verrill 1883; Wright and Studer 1889; Kükenthal 1919; Pasternak 1981; Watling et al. 2011). The genus

*Pseudochrysogorgia* Pante & France, 2010 only contains one species *P. bellona* Pante & France, 2010, and has a close relationship with *Metallogorgia* (Pante and France 2010).

During an investigation of the seamount benthic diversity in the Western Pacific Ocean and the South China Sea, we obtained 18 specimens of golden gorgonians. Based on morphological and phylogenetic analyses, they were described as one new species *Chrysogorgia carolinensis* sp. nov., and four known species, including *Chrysogorgia dendritica* Xu, Zhan & Xu, 2020, *Metallogorgia melanotrichos* (Wright & Studer, 1889), *Metallogorgia macropsina* Kükenthal, 1919 and *Pseudochrysogorgia bellona* Pante & France, 2010. Their phylogenetic positions are also discussed.

## Materials and methods

### Specimen collection and morphological examination

One specimen of *Chrysogorgia* Duchassaing & Michelotti, 1864 was collected from a seamount (tentatively named as M2) near the Mariana Trench by the ROV (remotely operated vehicle) *FaXian* (Discovery) in the tropical Western Pacific during the cruises of the R/V *KeXue* (Science) in 2016. One specimen of *Pseudochrysogorgia* Pante & France, 2010 was initially collected from the Ganquan Plateau in the South China Sea in 2018, unfortunately only a few frozen fragments of this specimen and a picture were obtained. Ten specimens of *Chrysogorgia* and six specimens of *Metallogorgia* Ver-sluys, 1902 were obtained from the seamounts (tentatively named as M5–M8) located on the Caroline Ridge during the cruises of the R/V *KeXue* (Science) in 2019. The *Chrysogorgia* and *Metallogorgia* specimens were photographed *in situ* before sampling, and photographed on board and then stored in 75% ethanol after collection. Small branches were detached and stored at -80 °C for molecular study.

The morphological terminology follows Bayer et al. (1983). The general morphology and anatomy were examined by using a stereo dissecting microscope. The sclerites of the polyps and branches were isolated by digestion of the tissues in sodium hypochlorite, and then were washed with deionized water repeatedly. Polyps and sclerites were air-dried and mounted on carbon double adhesive tape and coated for scanning electron microscopy (SEM) observation to investigate their structure. SEM scans were obtained and the optimum magnification was chosen for each kind of sclerite by using TM3030Plus SEM.

The type and voucher specimens have been deposited in the Marine Biological Museum of Chinese Academy of Sciences (MBMCAS) at Qingdao, China.

### DNA extraction and sequencing

Total genomic DNA was extracted from the polyps of each specimen using the TI-ANamp Marine Animal DNA Kit (Tiangen Bio. Co., Beijing, China) following the

manufacturer's instructions. PCR amplification for the mitochondrial genomic region 5'-end of the DNA mismatch repair protein – *mutS* – homolog (mtMutS) was conducted using primers AnthoCorMSH (5'-AGGAGAATTATTCTAAGTATGG-3'; Herrera et al. 2010) and Mut-3458R (5'-TSGAGCAAAGCCACTCC-3'; Sánchez et al. 2003). PCR reactions were performed as described by Xu et al. (2019). PCR purification and sequencing were performed by TsingKe Biological Technology (TsingKe Biotech, Beijing, China).

## Genetic distance and phylogenetic analyses

The mtMutS gene in octocorals was selected for molecular identification and phylogenetic analyses. All the available mtMutS sequences of *Chrysogorgia*, *Metallogorgia*, *Pseudochrysogorgia* and the out-group species from related chrysogorgioid and plexaurid genera were downloaded from GenBank, and those from duplicate isolates or without associated publications or not identified to species level were omitted from the molecular analyses. To correct possible mistakes, all the selected sequences were visually inspected, and translated to amino acids (AA) to insure all the AA sequences did not include stop codons and suspicious substitutions. The nucleotide and AA sequences were aligned using MAFFT v.7 (Katoh and Standley 2013) with the G-INS-i algorithm. With the guidance of the AA alignment, the nucleotide alignment was refined using BioEdit v7.0.5 (Hall 1999), and only the nucleotide alignment was used in the subsequent analyses. Genetic distances, calculated as uncorrected “p” distances within each species and among species, were estimated using MEGA 6.0 (Tamura et al. 2013).

For the phylogenetic analyses, only one known sequence was randomly selected from the conspecific sequences without genetic divergence (see Table 4). The TPM1uf+G evolutionary model was the best-fitted model for mtMutS, selected by AIC as implemented in jModeltest2 (Darriba et al. 2012). Maximum likelihood (ML) analysis was carried out using PhyML-3.1 (Guindon et al. 2010). For the ML bootstraps, we consider values < 70% as low, 70–94% as moderate and  $\geq$  95% as high following Hillis and Bull (1993). Node support came from a majority-rule consensus tree of 1000 bootstrap replicates. Bayesian inference (BI) analysis was carried out using MrBayes v3.2.3 (Ronquist and Huelsenbeck 2003) on CIPRES Science Gateway. Posterior probability was estimated using four chains running 10,000,000 generations sampling every 1000 generations. The first 25% of sampled trees were considered burn-in trees. Convergence was assessed by checking the standard deviation of partition frequencies (< 0.01), the potential scale reduction factor (ca. 1.00), and the plots of log likelihood values (no obvious trend was observed over time). For the Bayesian posterior probabilities, we consider values < 0.95 as low and  $\geq$  0.95 as high following Alfaro et al. (2003). The museum voucher specimen and GenBank accession numbers of the mtMutS sequences were listed next to the species names in the phylogenetic trees (Figure 21).

## Results

### Class Anthozoa Ehrenberg, 1834

#### Subclass Octocorallia Haeckel, 1866

#### Order Alcyonacea Lamouroux, 1812

#### Suborder Calcaxonia Grasshoff, 1999

#### Family Chrysogorgiidae Verrill, 1883

### Genus *Chrysogorgia* Duchassaing & Michelotti, 1864

**Diagnosis (based on Xu et al. 2020).** Colony branching usually sympodial, occasionally monopodial, arising from a single ascending spiral (clockwise or counterclockwise, bottlebrush-shaped colony), a fan (planar colony), two fans emerging from a short main stem (biflabellate colony), or an unbranched main stem forming a tree-shaped colony. Axis with a metallic shine, dark to golden in color. Branch subdivided dichotomously or pinnately. Most polyps relatively large to the size of the branches they sit on, few in number and well separated from one another. Sclerites in the form of spindles, rods, scales, and rare plates with little ornamentation.

**Type species.** *Chrysogorgia desbonni* Duchassaing & Michelotti, 1864, by monotypy.

**Distribution.** Worldwide in a depth range of 10–4492 m (Watling et al. 2011).

### *Chrysogorgia dendritica* Xu, Zhan & Xu, 2020

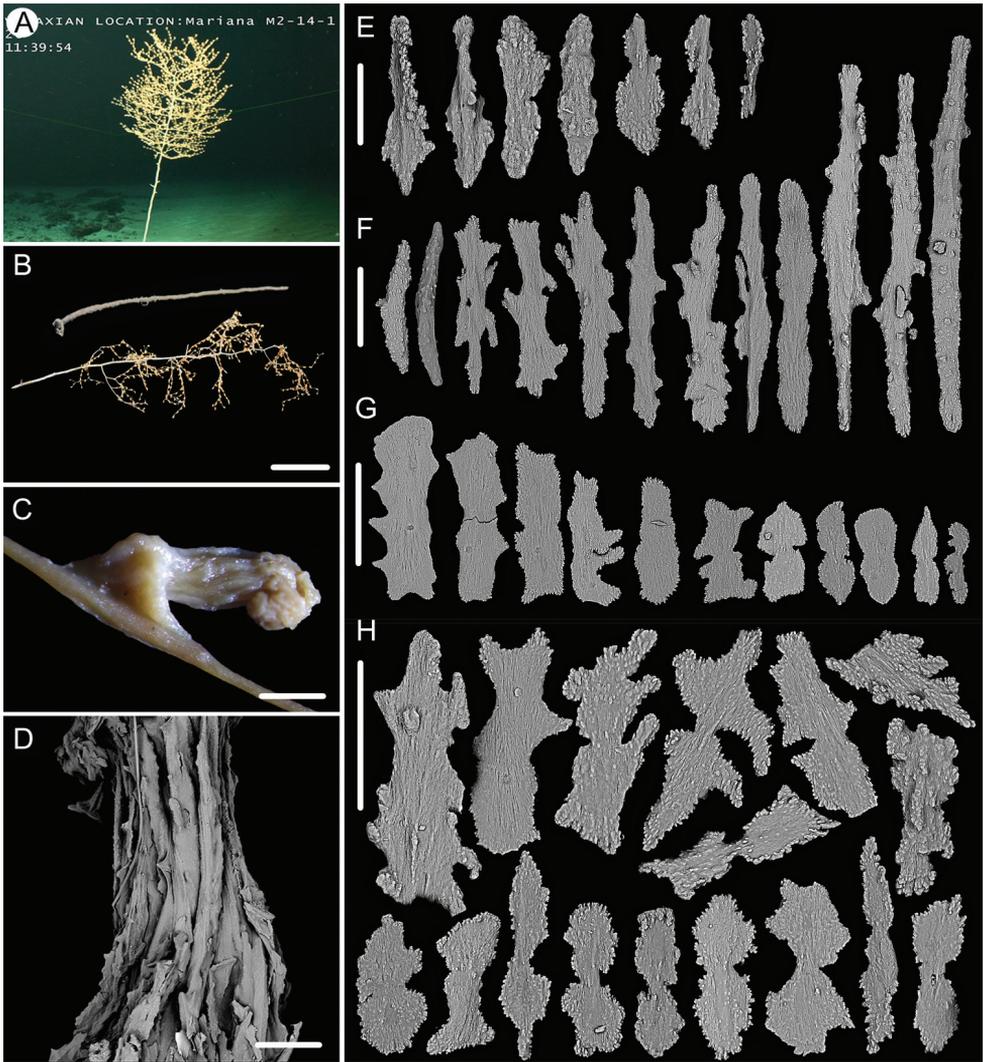
Figures 1–4; Table 1

*Chrysogorgia dendritica* Xu, Zhan & Xu, 2020: 6–8, figs 2, 3.

**Type locality.** Kocebu Guyot in the Magellan Seamount chain, 1821 m depth.

**Voucher specimens.** MBM286353, station FX-Dive 71 (11°20.83'N, 139°15.87'E), a seamount (tentatively named as M2) near the Mariana Trench, depth 1375 m, 28 March 2016. MBM286442, station FX-Dive 211 (10°02.97'N, 140°10.48'E), a seamount (tentatively named as M5) located on the Caroline Ridge, depth 1475 m, 29 May 2019. MBM286443, station FX-Dive 211 (10°03.27'N, 140°10.70'E), a seamount (M5) located on the Caroline Ridge, depth 1387 m, 29 May 2019. MBM286444, station FX-Dive 227 (10°37.92'N, 140°05.62'E), a seamount (tentatively named as M8) located on the Caroline Ridge, depth 1702 m, 15 June 2019. GenBank accession number: MT269888.

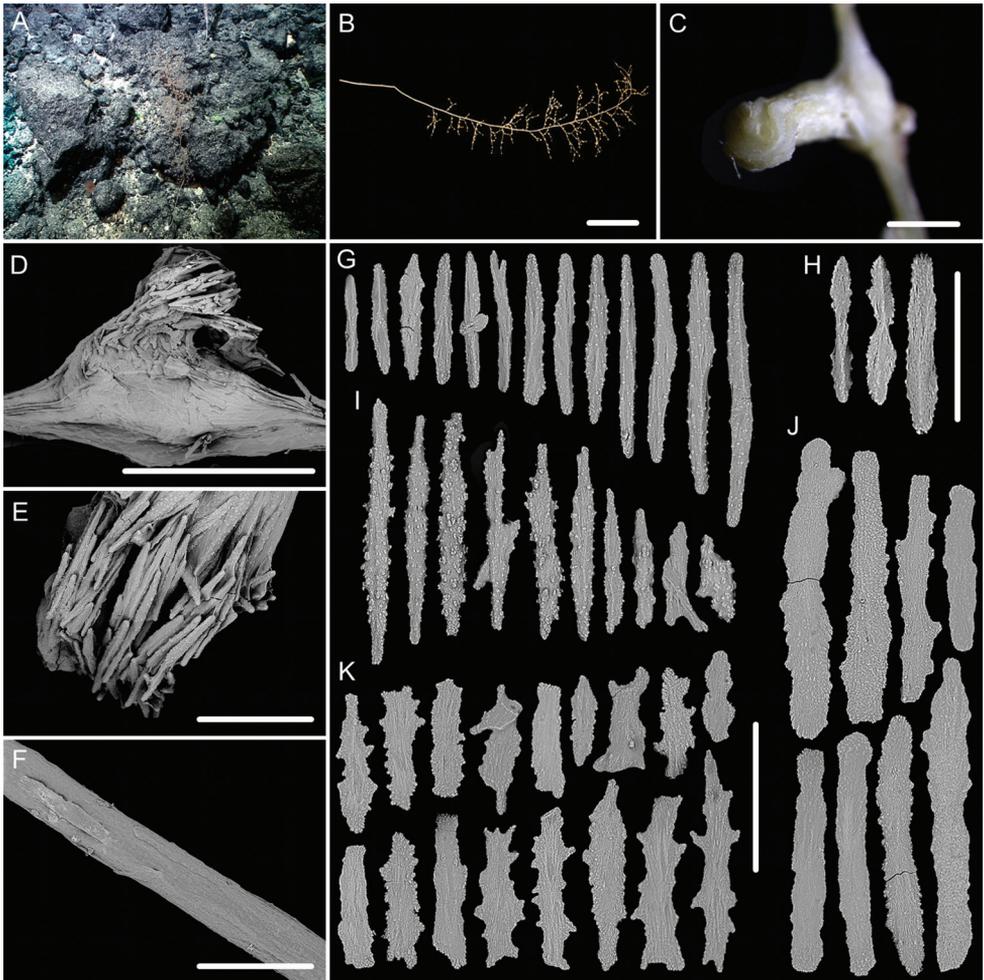
**Extended diagnosis.** *Chrysogorgia* “group A, Spiculosae” with 1/3L Branching sequence and a monopodial or a little zigzagging stem. Juvenile with a bottlebrush-like colony, while adult usually having a tree-shaped colony. Branches nearly perpendicular to stem, subdivided dichotomously. Polyps with a long neck and an expanded base.



**Figure 1.** External morphology, polyps and sclerites of *Chrysogorgia dendritica* MBM286353 **A, B** the tree-shaped colony *in situ* and after collection (likely an adult), with a broken stem and a branching part **C** a single polyp under a light microscope **D** long polyp neck under SEM **E** sclerites in tentacles **F** sclerites of the polyp neck **G** sclerites in coenenchyme **H** sclerites at the basal polyp body. Scale bars: 10 cm (**B**); 1 mm (**C**); 200  $\mu$ m (**D**); 50  $\mu$ m (**E**), 100  $\mu$ m (**F, G, H**).

Rods and rare scales in tentacles, longitudinally arranged. Rods/spindles and elongate scales in polyp neck longitudinally arranged, coarse with many warts on surface. Scales and rare plates at the basal polyp body irregularly and alternately arranged, irregular and often amoeba-shaped. Scales in coenenchyme sparse and elongate, usually lobed with irregular edges.

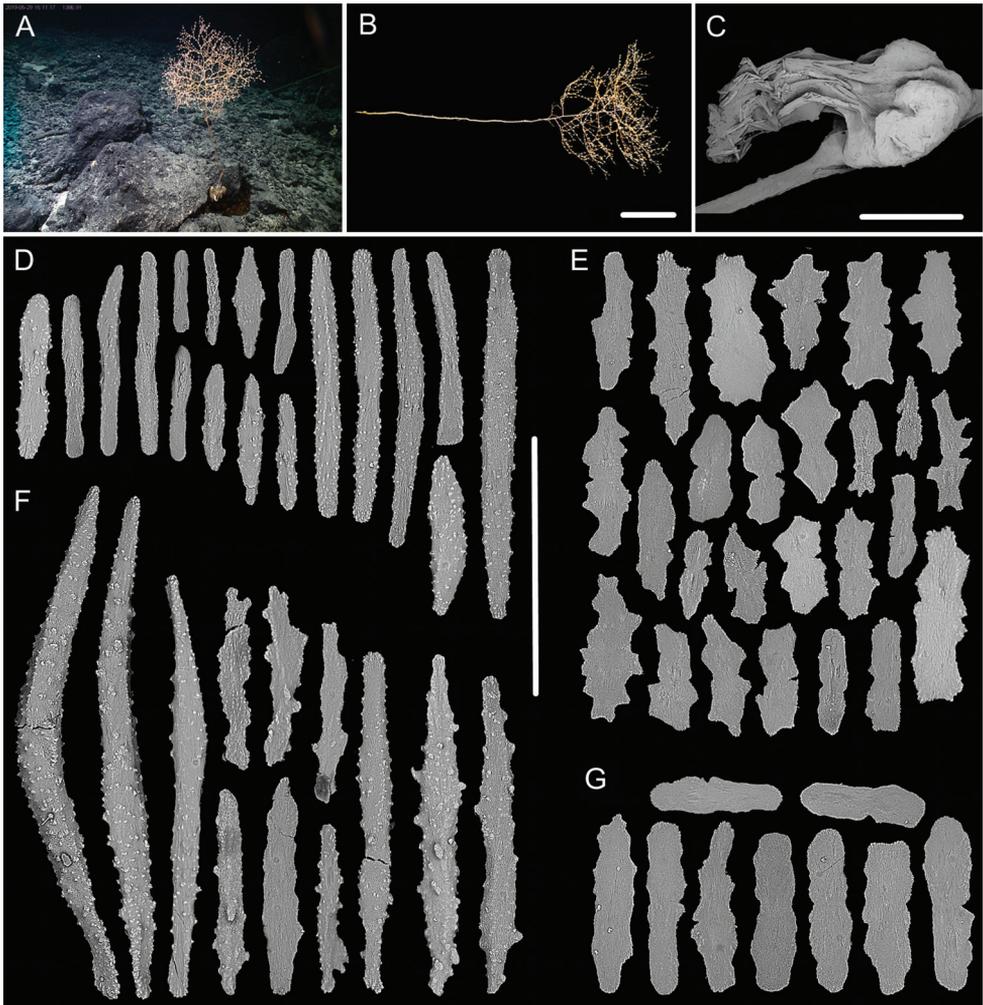
**Description.** For morphological measurements, see Table 1.



**Figure 2.** External morphology, polyps and sclerites of *Chrysogorgia dendritica* MBM286442 **A, B** the bottlebrush-like colony *in situ* and after collection (likely a juvenile) **C** a single polyp under a light microscope **D** a single polyp under SEM **E** tentacular part under SEM **F** coenenchyme under SEM **G** sclerites in tentacles **H** sclerites extending to pinnules **I** sclerites of the polyp neck **J** sclerites in coenenchyme **K** sclerites at the basal polyp body. Scale bars: 10 cm (**B**); 1 mm (**C, D**); 300  $\mu$ m (**E, F**); 200  $\mu$ m (**G, I–K** at the same scale), 100  $\mu$ m (**H**).

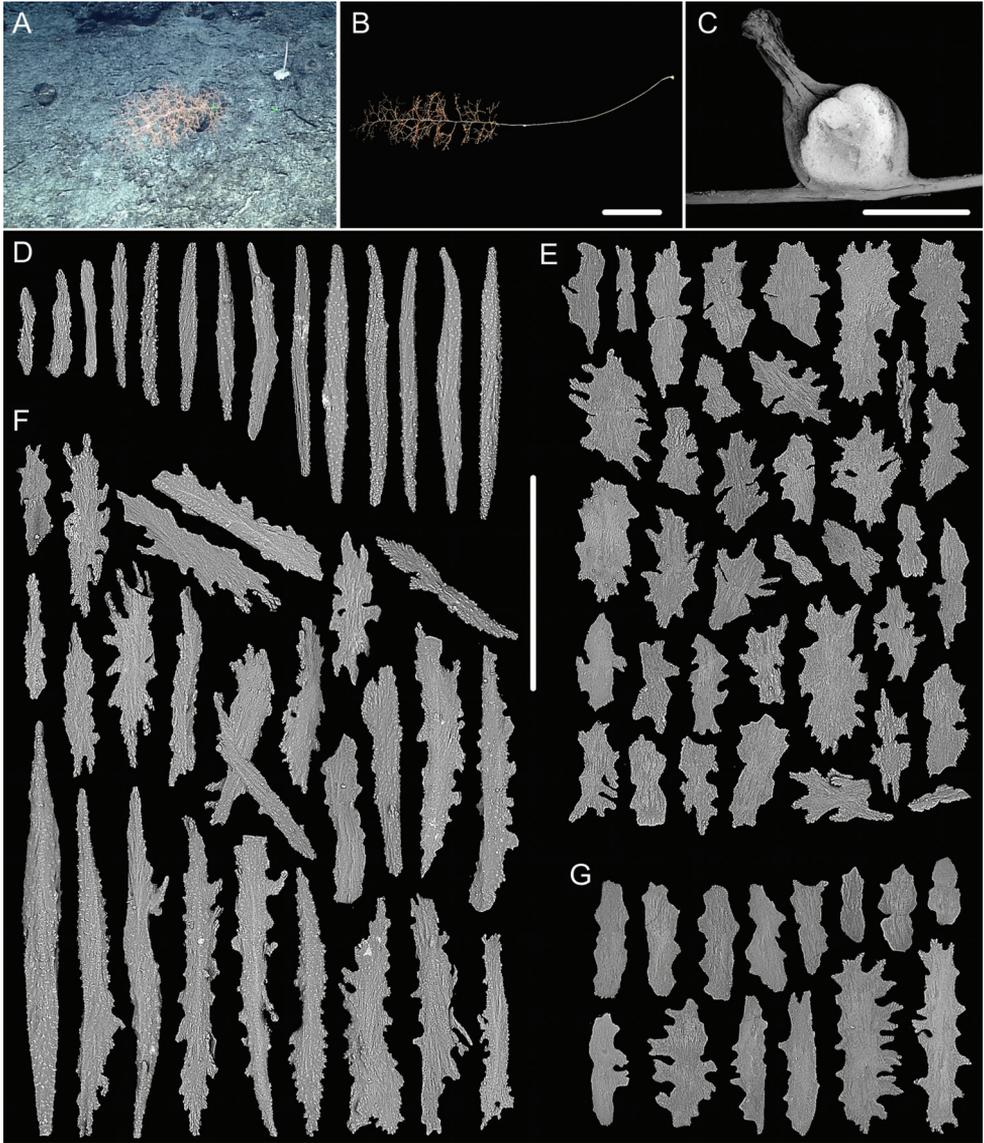
**Distribution.** Kocebu Guyot, 1821 m (Xu et al. 2020); a seamount adjacent to the Mariana Trench and seamounts on the Caroline Ridge, 1375–1702 m depth.

**Remarks.** The four specimens match the holotype of *Chrysogorgia dendritica* Xu, Zhan & Xu, 2020 in having a monopodial stem and the same sclerite form, for example, rods and rare scales in tentacles, rods/spindles and elongate scales in polyp neck, irregular scales at the basal polyp body, and elongate scales in coenenchyme. Moreover, their mtMutS gene sequences are identical (see the genetic analysis below). Thus, we identified the four specimens as *C. dendritica*. The sclerites in the four



**Figure 3.** External morphology, polyps and sclerites of *Chrysogorgia dendritica* MBM286443 **A, B** the tree-shaped colony *in situ* and after collection (likely an adult) **C** a single polyp under SEM **D** sclerites in tentacles **E** sclerites at the basal polyp body **F** sclerites of the polyp neck **G** sclerites in coenenchyme. Scale bars: 10 cm (**B**); 1 mm (**C**); 300  $\mu$ m (**D–G** at the same scale).

voucher specimens and the holotype showed some differences: (1) rod-like scales with an obvious medial contraction often present in MBM286353 and MBM286442, while rare in the holotype, MBM286443 and MBM286444 (Figures 1A, 2H vs. Figures 3D, 4D); (2) large cured spindles are rarely present in the polyp neck of the holotype, MBM286443 and MBM286444, while absent in the other two specimens (Figures 3F, 4F vs. Figures 1F, 2I); (3) scales at the basal polyp body of the holotype and MBM286444 are more irregular and amoeba-shaped than the other specimens (Figure 4E vs. Figures 1H, 2K, 3E); and (4) scales in coenenchyme are more elongate in MBM286442 than the other specimens (Figure 2J vs. Figures 1G, 3G, 4G).



**Figure 4.** External morphology, polyps and sclerites of *Chrysogorgia dendritica* MBM286444 **A, B** the colony *in situ* and after collection (likely an intermediate state) **C** a single polyp under SEM **D** sclerites in tentacles **E** sclerites of the polyp neck **F** sclerites at the basal polyp body **G** sclerites in coenenchyme. Scale bars: 20 cm (**B**); 2 mm (**C**); 300  $\mu$ m (**D–G** at the same scale).

However, these differences are minor and not constant, and we thus treat as the conspecific variation.

The four specimens of *C. dendritica* showed a series of growth stages, from bottle-brush-like colony (juvenile) to tree-shaped colony (adult). Considering the diameter size of the stem base and scars on the stem, the specimen MBM286442 is likely a

juvenile with a narrow stem and without scars, while the other specimens have wider stems and some old scars of the past branches (Table 1). The juvenile has a bottlebrush-like colony (Figure 2B), while the adult has a long monopodial stem with branches occurring on the top, forming a tree-shaped colony (Figures 1B, 3B). Compared to the changing colony shapes, the sclerite forms showed small variation in the growth stages and can be used as a main character to identify the species.

***Chrysogorgia carolinensis* sp. nov.**

<http://zoobank.org/A37B30BA-6396-4679-9D39-1FFB51FCCD4D>

Figures 5, 6; Table 1

**Type material. Holotype.** MBM286494, station FX-Dive 226 (10°38.18'N, 140°04.08'E), a seamount (tentatively named as M8) located on the Caroline Ridge, depth 1832 m, 14 June 2019. GenBank accession number: MT269889.

**Paratypes.** MBM286493, station FX-Dive 224 (10°37.63'N, 140°05.45'E), depth 1509 m, 12 June 2019. MBM286495, station FX-Dive 227 (10°37.92'N, 140°05.62'E), depth 1709 m. MBM286496, station FX-Dive 227 (10°37.92'N, 140°05.62'E), depth 1706 m, 15 June 2019. MBM286497, station FX-Dive 227 (10°37.90'N, 140°05.62'E), depth 1695 m, 15 June 2019. MBM286498, station FX-Dive 227 (10°37.68'N, 140°05.48'E), depth 1537m, 15 June 2019. MBM286499, station FX-Dive 227 (10°37.60'N, 140°05.43'E), depth 1506 m, 15 June 2019. They were all collected from a seamount (tentatively named as M8) located on the Caroline Ridge.

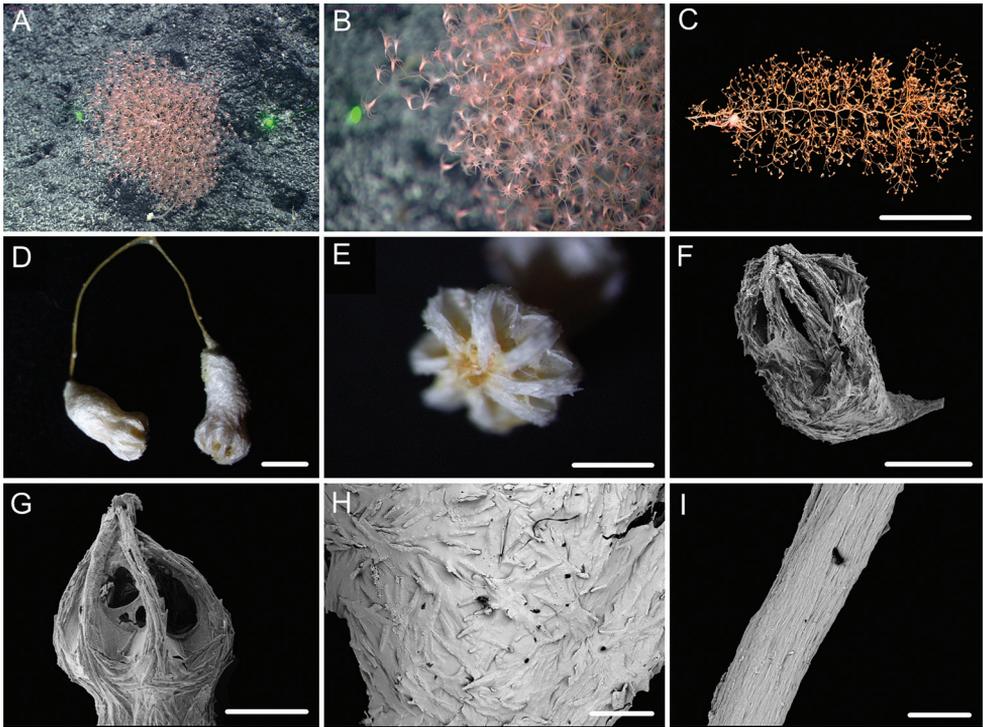
**Diagnosis.** *Chrysogorgia* “group A, Spiculosae” with 1/3L branching sequence. Branches subdivided dichotomously, up to sixth order. Polyps only present in the end of terminal branchlets. Polyps large with pitcher shape, up to 8 mm long. Rods and spindles slender and coarse with many warts on surface in the back and base of tentacles. Scales amoeba-shaped, branched toward to any directions, irregularly and alternately arranged at basal polyp body. Scales rare, transversally arranged in coenenchyme.

**Description.** Specimen of holotype ca. 31 cm long and 14 cm wide excluding the holdfast (Figure 5C). Colony bottlebrush-shaped, with branching sequence 1/3L. Stem golden with metallic luster, ca. 1 mm in diameter at base. Branches subdivided dichotomously, up to sixth order, with distance between adjacent branches 6–12 mm long and orthostiche interval 19–35 mm long in measurements from all specimens. Branches up to 6 cm with the first branch internodes 7–15 mm long and terminal branchlets up to 2 cm long. Polyps only present in the end of the terminal branchlets. Polyps large with pitcher shape, some of them contracted and narrow at the base of tentacles, average 5 mm long with the terminal one up to 8 mm long, and 1–3 mm wide (Figure 5B, D, F). No polyps in axis internodes.

Rods and spindles slender and coarse with many warts on surface, some of them branched, rarely with one end a little flat, longitudinally arranged in the back of tentacles and usually forming eight distinct columns, and transversally or longitudinally arranged in the base of tentacles, measuring 107–814 × 10–78 μm (length × width,

**Table 1.** Morphological comparisons between *Chrysoyorgia carolinensis* sp. nov., *Chrysoyorgia dendritica* Xu, Zhan & Xu, 2020 and *Chrysoyorgia abludo* Pante & Watling, 2012, including detailed morphological measuring data of five specimens of *C. dendritica*.

| Characters/species                         | <i>Chrysoyorgia dendritica</i>              |  |  |   | <i>Chrysoyorgia carolinensis</i> sp. nov.             |   | <i>Chrysoyorgia abludo</i> |   |                 |
|--|---|--|--|---|---|---|----------------------------|---|-----------------|
|  | holotype                                    | MBM286353  | MBM286442  | MBM286443   | MBM286444   | holotype                                      | A                          | holotype                                  | paratype        |
| Specimen Group type                        |   |  | A  |   |   | A   |                            | A   |                 |
| Branching sequence                         |   |  | 1/3L   |   |   | 1/3L  |                            | 1/3, 1/4L, irregular                      |                 |
| Axis                                       |   |  | monopodial, or a little zigzagging                     |   |   | symptodial                                    |                            | monopodial                                |                 |
| Colony shape                               | tree-shaped                                 | tree-shaped  | bottlebrush-like                                       | tree-shaped   | a little tree-shaped                                  | bottlebrush-shaped                            |                            | bottlebrush-shaped                        | tree-shaped     |
| Colony height (cm)                         | 57  | 85.5   | 55   | 50  | 110   | 31  |                            | 16  | 50              |
| Basal stem width (mm)                      | 2   | 7  | 1.2  | 3   | 3   | 1   |                            | No data                                   | 2.2             |
| Interbranch distance (mm)                  | 16–22                                       | 18   | 5–22   | 11–15   | 12–24   | 6–12  |                            | 4.3–6.8                                   | 7.5–15.0        |
| Orthostiche interval (mm)                  | 50–55                                       | 50–55  | 37–47  | 36–47   | 44–61   | 19–35   |                            | No data                                   | No data         |
| First branch internode (mm)                | 15–20                                       | 14–22  | 11–20  | 9–23  | 20–30   | 7–15  |                            | 6.1–11.0                                  | 16              |
| Polyps on internodes                       | 1–5   | 2–3  | 1–3  | 1–4   | 1–4   | 0   |                            | 1–2                                       | No data         |
| Polyps on terminal branchlets              | 1–6   | 1–4  | 1–4  | 1–8   | 1–8   | 1   |                            | 1–3                                       | 1–6             |
| Polyps height (mm)                         | 3   | 3–5  | 1.5–2.0  | 2–3   | 3–4   | 3–8, average 5                                |                            | 0.8–2.2                                   | 0.8–2.2         |
| Sclerites in coenenchyme ( $\mu\text{m}$ ) | flat elongate scales often with lobed edges | 82–200 × 10–96                                       | 139–420 × 16–112                                       | 92–266 × 15–57  | 53–379 × 10–34  | elongate scales occasionally with lobed edges |                            | small rugged scales with less lobed edges | scales and rods |
| Sclerites in body wall ( $\mu\text{m}$ )   | scales, rods and spindles                   | 68–190 × 7–58 at basal body; 171–516 × 20–55 in neck | 100–306 × 20–72 at basal body; 121–353 × 12–56 in neck | 80–229 × 13–82 at basal body; 207–614 × 14–76 in neck | 39–236 × 8–128 at basal body; 137–590 × 12–98 in neck | scales, rods and spindles                     |                            |   |                 |
| Sclerites in tentacles ( $\mu\text{m}$ )   | scales and rods                             | 74–135 × 4–32  | 105–365 × 6–45   | 75–429 × 10–43  | 93–275 × 24–93  | rods and spindles                             |                            | rods                                      |                 |
| Distribution                               | Koebu Guyot                                 | an unmaimed seamount adjacent to the Mariana Trench  | unnamed seamounts on the Caroline Ridge                | unnamed seamounts on the Caroline Ridge               | unnamed seamount on the Caroline Ridge                | an unmaimed seamount on the Caroline Ridge    |                            | North Atlantic                            |                 |
| References                                 | Xu et al. 2020                              |  | Present study  | Present study   | Present study   | Present study                                 |                            | Pante and Watling 2012                    |                 |



**Figure 5.** External morphology and polyps of *Chrysogorgia carolinensis* sp. nov. **A** the holotype *in situ* **B** close-up branches *in situ* **C** the holotype after collection **D** two polyps under a light microscope **E** tentacles under a light microscope **F** a single polyp under SEM **G** upper part of a polyp under SEM **H** basal polyp body under SEM **I** coenenchyme under SEM. Scale bars: 10 cm (**B**); 2 mm (**D**); 1 mm (**E–G**); 300  $\mu$ m (**H**); 100  $\mu$ m (**I**).

the same below, Figures 5E, G, 6A). Rare sclerites extend into pinnules, but mostly pinnules free of sclerites. Scales amoeba-shaped, branched in any directions, irregularly and alternately arranged at the basal polyp body, and measuring 161–483  $\times$  14–170  $\mu$ m (Figures 5H, 6B). Scales rare and elongate, some of them lobed with irregular edges, transversally arranged in coenenchyme, and measuring 139–221  $\times$  29–67  $\mu$ m (Figures 5I, 6C).

**Type locality.** A seamount (tentatively named as M8) located on the Caroline Ridge with a depth range of 1506–1832 m.

**Etymology.** Named after the type locality, the Caroline Ridge, where the species was discovered.

**Distribution and habitat.** Found only from a seamount located on the Caroline Ridge. Colony attached to a rocky substrate (Figure 5A).

**Remarks.** *Chrysogorgia carolinensis* sp. nov. belongs to the “group A, Spiculosaes” with an unusual branching sequence of 1/3L and bottlebrush-shaped colony, which is similar to *C. midas* Cairns, 2018 and *C. abludo* Pante & Watling, 2012. However, the new species differs distinctly from these species by the presence of amoeba-shaped scales, which branch toward to any directions at the basal polyp body (vs. absence in



**Figure 6.** Sclerites of *Chrysogorgia carolinensis* sp. nov. **A** sclerites in the back and at the base of tentacles **B** sclerites at the basal polyp body **C** sclerites in coenenchyme. Scale bar: 300  $\mu\text{m}$  (all images at the same scale).

both species). *Chrysogorgia carolinensis* sp. nov. is also similar to *C. dendritica* by 1/3L branching sequence and the conspicuously amoeba-shaped sclerites at the basal polyp body. However, the new species is easily separated by the bottlebrush-shaped colony (vs. tree-shaped), absence of polyps on internodes (vs. presence) and larger polyps up to 8 mm long (vs. no more than 5 mm) (Table 1).

### Genus *Metallogorgia* Versluys, 1902

**Diagnosis (based on Versluys 1902; Nutting 1908; Kükenthal 1919).** Main stem monopodial with a few branches occurring on the side. Axis round and solid with a smooth surface and strong metallic luster. Branches irregular, subdivided dichotomously with branchlets forming a sympodium. The coenenchyme usually thin with a few sclerites or not well differentiated this layer.

**Type species.** *Metallogorgia melanotrichos* (Wright & Studer, 1889)

**Distribution.** Atlantic Ocean, Pacific Ocean and Indian Ocean, in a depth range of 567–2311 m (Watling et al. 2011, and the present study).

***Metallogorgia melanotrichos* (Wright & Studer, 1889)**

Figures 7–10; Tables 2, 3

*Dasygorgia melanotrichos* Wright & Studer, 1889: 15, pl. IV, fig. 3, pl. V, fig. 5.

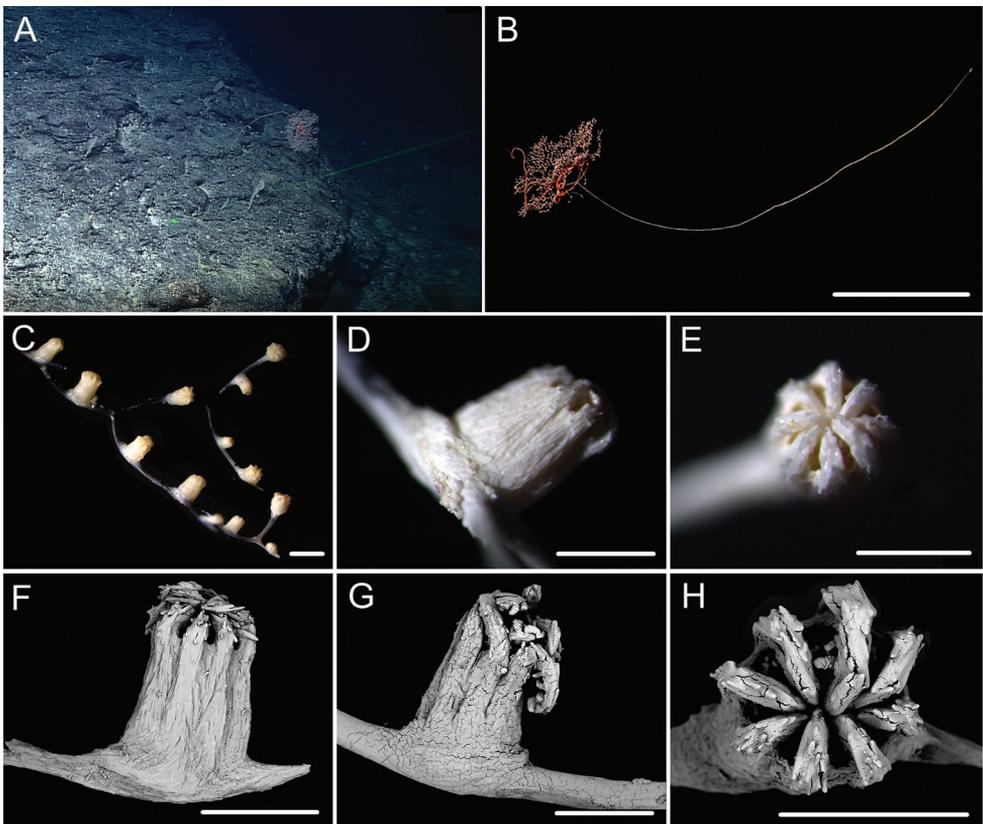
*Metallogorgia melanotrichos*: Versluys, 1902: 87.

*Metallogorgia melanotrichos*: Nutting, 1908: 593–594, pl. LI, fig. 5.

*Metallogorgia melanotrichos*: Kükenthal, 1919: 503.

*Metallogorgia melanotrichos*: Pasternak, 1981: 51.

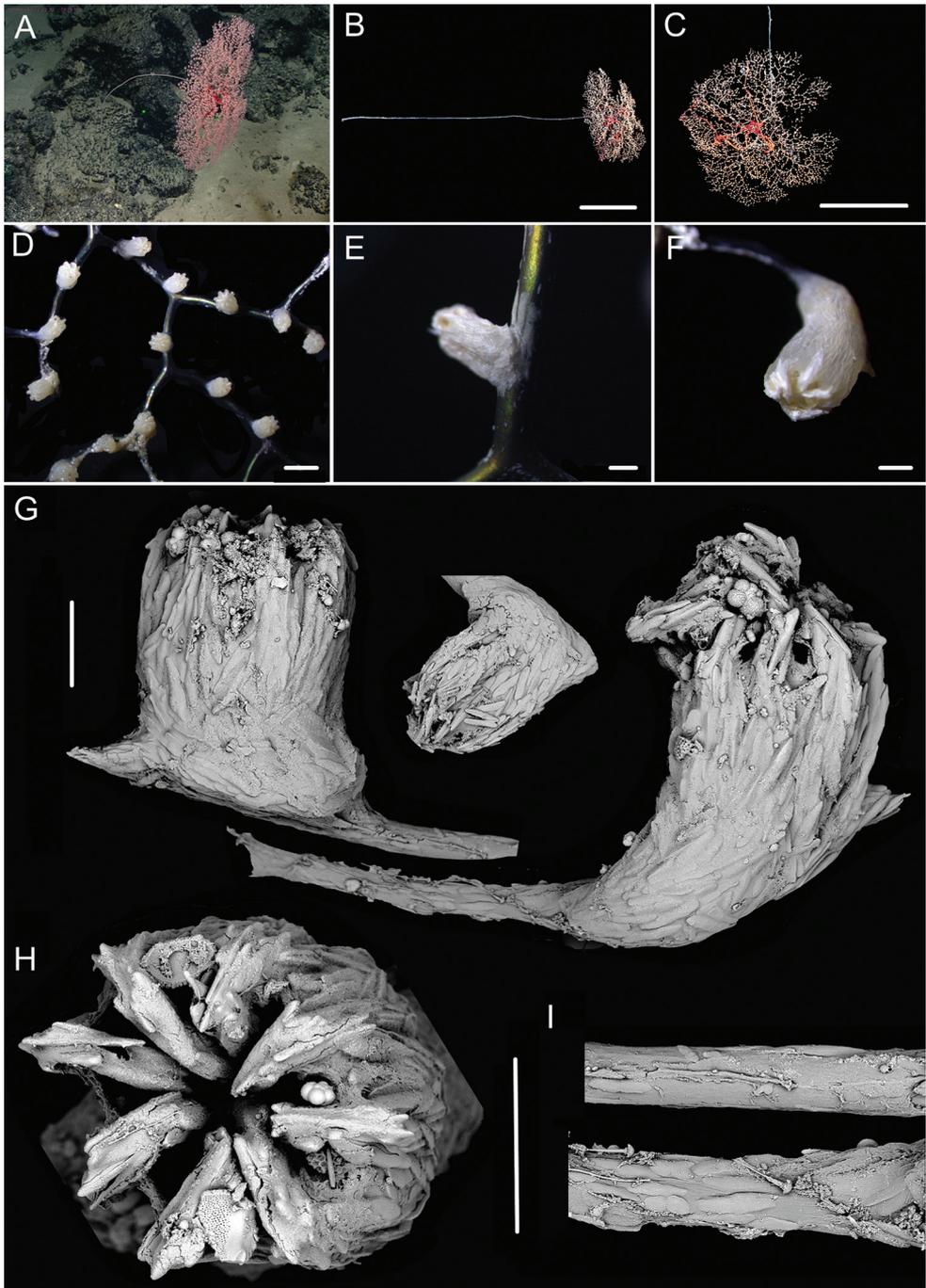
**Type locality.** Ascension Island in the South Atlantic Ocean, 778 m depth (Wright and Studer 1889).



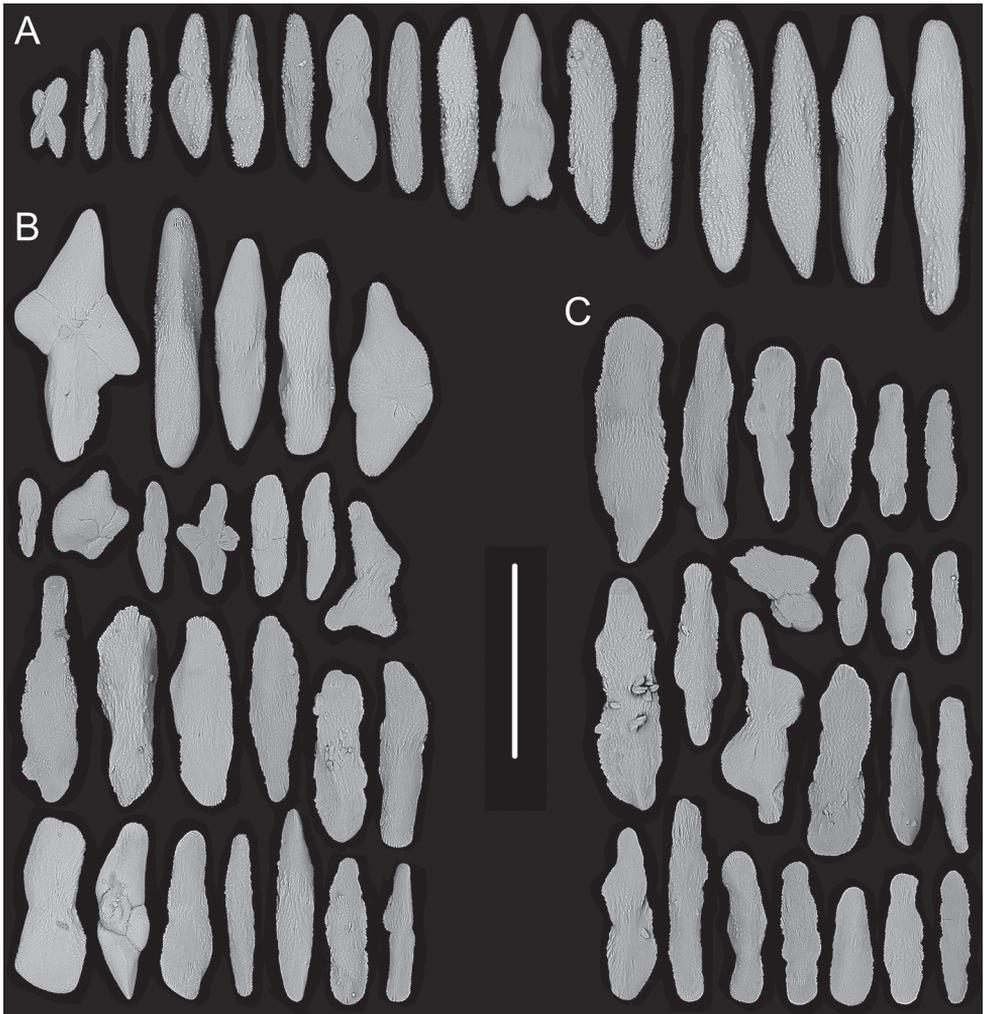
**Figure 7.** External morphology and polyps of *Metallogorgia melanotrichos* MBM286485 **A** the colony *in situ*. Laser dots spaced at 33 cm used for scale **B** the colony after collection **C** a branch under a light microscope **D, E** a single polyp under a light microscope **F, G** a single polyp under SEM **H** head of one polyp under SEM. Scale bars: 20 cm (**B**), 2 mm (**C**), and 1 mm (**E–H**).



**Figure 8.** Sclerites of *Metallogorgia melanotrichos* MBM286485 **A** rods in tentacles **B** rods and scales in the polyp-body wall **C** scales in coenenchyme. Scale bar: 200  $\mu\text{m}$  (all images at the same scale).



**Figure 9.** External morphology and polyps of *Metallogorgia melanotrichos* MBM286486 **A** the colony *in situ*. Laser dots spaced at 33 cm used for scale **B, C** the colony after collection **D** a branch under a light microscope **E, F** a single polyp under a light microscope **G** three polyps under SEM **H** head of one polyp under SEM **I** coenenchyme under SEM. Scale bars: 10 cm (**B, C**), 2 mm (**D**) and 500  $\mu$ m (**E–I, H, I** at the same scale).



**Figure 10.** Sclerites of *Metallogorgia melanotrichos* MBM286486 **A** rods in tentacles **B** rods and scales in the polyp-body wall **C** scales in coenenchyme. Scale bar: 300  $\mu$ m (all images at the same scale).

**Voucher specimens.** MBM286485, station FX-Dive 222 (10°04.73'N, 140°09.45'E), depth 1839 m, 10 June 2019; MBM286486, station FX-Dive 227 (10°37.92'N, 140°05.62'E), depth 1706 m, 15 June 2019. They were collected from two seamounts (tentatively named as M5 and M8, respectively) located on the Caroline Ridge in the West Pacific Ocean.

**Diagnosis (extended on the basis of Versluys 1902; Kükenthal 1919; Mosher and Watling 2009).** In adults, main stem monopodial with a few large branches occurring on the distal end. Branching angle between these large branches usually obtuse. In each large branch, strong branchlets subdivided dichotomously and forming a sympodium pattern. In juveniles, main stem monopodial and gracile with branches

producing on the lateral of the trunk randomly and subdivided dichotomously in multiple planes. Polyps conical or cylindrical, absent on the stem of adults but present in juveniles. Sclerites elongated and often crossed, arranged densely in polyps and relatively sparsely in coenenchyme. Rods longitudinally arranged in tentacles, covered with sparse fine warts. Rods longitudinally arranged on upper part of polyp body, and scales partially crosswise or transversely arranged on bottom, with nearly smooth surface. Scales transversely arranged in coenenchyme, usually with rounded ends and occasionally irregular edges. Nematozooids absent.

**Description.** For morphological measurements, see Table 2.

**Distribution.** Central Indo-Pacific Ocean (Wright and Studer 1889; Versluys 1902), Western and Central Pacific (Nutting 1908; Pasternak 1981; present study), Atlantic Ocean, 183–2265 m depth (Kükenthal 1919; Watling et al. 2011; Pante et al. 2012).

**Remarks.** *Metallogorgia melanotrichos* (Wright & Studer, 1889) is characterized by its completely monopodial stem, with the branches in adults occurring on the distal end, and scales in both body wall and coenenchyme (Table 3). Furthermore, *M. melanotrichos* has a much more extensive distribution than its congeners, while other species have a relatively limited distribution. Our specimens match well with the original description in the sclerites, but possess a relatively larger polyp (most 2 mm, up to

**Table 2.** The morphological measuring data of the specimens of *Metallogorgia*. “–” means nonexistent or meaningless data.

| Characters/ Specimens                  | MBM286485               | MBM286486               | MBM286484            | MBM286487            | MBM286488            | MBM286489            |
|--|-------------------------|-------------------------|----------------------|----------------------|----------------------|----------------------|
| Species                                | <i>M. melanotrichos</i> | <i>M. melanotrichos</i> | <i>M. macrospina</i> | <i>M. macrospina</i> | <i>M. macrospina</i> | <i>M. macrospina</i> |
| Colony height (cm)                     | 76                      | 35                      | 56                   | 51                   | 69                   | 48                   |
| Basal stem width (mm)                  | 2.7                     | 1.5                     | 1.0                  | 2.5                  | 3.0                  | 2.5                  |
| Branching part height (cm)             | 9                       | 8                       | –                    | 12                   | 11                   | 7                    |
| Branching part width (cm)              | 18                      | 18                      | 6                    | 26                   | 20                   | 14                   |
| Branch maximal length (cm)             | 10                      | 12                      | 4                    | 16                   | 13                   | 12                   |
| Branches                               | 2                       | 2                       | 22                   | 14                   | 7                    | 6                    |
| Interbranch distance (mm)              | –                       | –                       | 9–25                 | 6–13                 | 13–18                | 5–18                 |
| Internode length (mm)                  | 4–12                    | 3–11                    | 3–7                  | 3–8                  | 3–10                 | 3–11                 |
| First internode length (mm)            | 13–24                   | 12–18                   | 3–8                  | 5–8                  | 6–8                  | 6–11                 |
| Polyp height (mm)                      | 1.0–2.5                 | 1.0–4.0, most 2.0       | 1.0–2.5, most 1.0    | average 1.0          | 1.0–1.5              | 1.0–1.5              |
| Polyps in internode                    | 1, rarely 2             | 1, rarely 2             | 1, rarely 2          | 1, rarely 2          | 1, rarely 2          | 1, rarely 2          |
| Polyps in terminal branchlets          | 1–3                     | 1–4                     | 1–4                  | 1–4                  | 1–5                  | 1–2                  |
| Inter-polyp distance (mm)              | 1–6                     | 1–4                     | 2–5                  | 1–3                  | 0–5                  | 0–4                  |
| Sclerites measured in tentacles (µm)   | 129–433 × 17–55         | 125–467 × 21–125        | 96–450 × 10–85       | 44–542 × 6–117       | 120–492 × 12–98      | 115–460 × 14–78      |
| Sclerites measured in body wall (µm)   | 172–571 × 14–93         | 128–429 × 25–125        | 96–450 × 10–85       | 44–542 × 6–117       | 137–473 × 17–93      | 57–417 × 11–66       |
| Sclerites measured in coenenchyme (µm) | 96–378 × 18–66          | 148–379 × 31–113        | 112–456 × 10–62      | 175–394 × 17–75      | 78–328 × 11–51       | 70–372 × 14–50       |
| Figures                                | 7, 8                    | 9, 10                   | 11, 12               | 13, 14               | 15, 16               | 17, 18               |

**Table 3.** The comparisons of the species (adults) in the genus *Metallogorgia* Versluys, 1902 and *Pseudochrysgorgia bellona* Pante & France, 2010.

| Characters/ Species                      | <i>M. macrospina</i>  | <i>M. melanotrichos</i>  | <i>M. splendens</i> *   | <i>M. tenuis</i>  | <i>P. bellona</i>                         |
|--|---|--|---|---|---|
| Branching part                           | sympodial   | monopodial   | unknown   | sympodial*  | monopodial                                |
| Branchlets forming a sympodium           | yes   | yes  | unknown   | No*   | No  |
| Interbranch distance (mm)                | 5–18  | –  | unknown   | 10–18*  | 9.9–17.2                                  |
| Polyp height (mm)                        | 1–1.5   | 1.5–2.0  | 1.5   | 1.5–2.0   | 1.0–3.3                                   |
| Sclerites in tentacles                   | rods  | rods   | plates  | spindles  | rods                                      |
| Sclerites in body wall                   | rods  | rods and scales  | rods  | rods and spindles   | rods and scales                           |
| Sclerites with its shapes in coenenchyme | rods and scales elongated with slightly serrated edges and coarse surface | scales elongated with relatively smooth edges and surface  | rods small, flattened, often with serrated edges and smooth surface | scales small, elongated, often with irregular shape and serrated edges. | scales and plates with many ornamentation |
| Dendritic holdfast                       | no  | no   | unknown   | no  | yes                                       |
| Reference                                | Kükenthal 1919, present study   | Wright and Studer 1889, Versluys 1902, Nutting 1908, Kükenthal 1919, Pasternak 1981, present study | Verrill 1883, Versluys 1902, Kükenthal 1919, Deichmann 1936         | Pasternak 1981  | Pante and France 2010, present study      |

\*, putative species or questionable regarded by Watling et al. 2011.

4 mm vs. 1.75 mm), and longer scales in coenenchyme (up to 379  $\mu\text{m}$  vs. 225  $\mu\text{m}$ ) (Kükenthal 1919, Table 2). The branches of the specimen MBM286486 on one side is irregular and tend to form a fake spiral with branches subdivided dichotomously in multiple planes, while it is regular and forms a planar layer that nearly perpendicular to the trunk in the specimen MBM286485.

### *Metallogorgia macrospina* Kükenthal, 1919

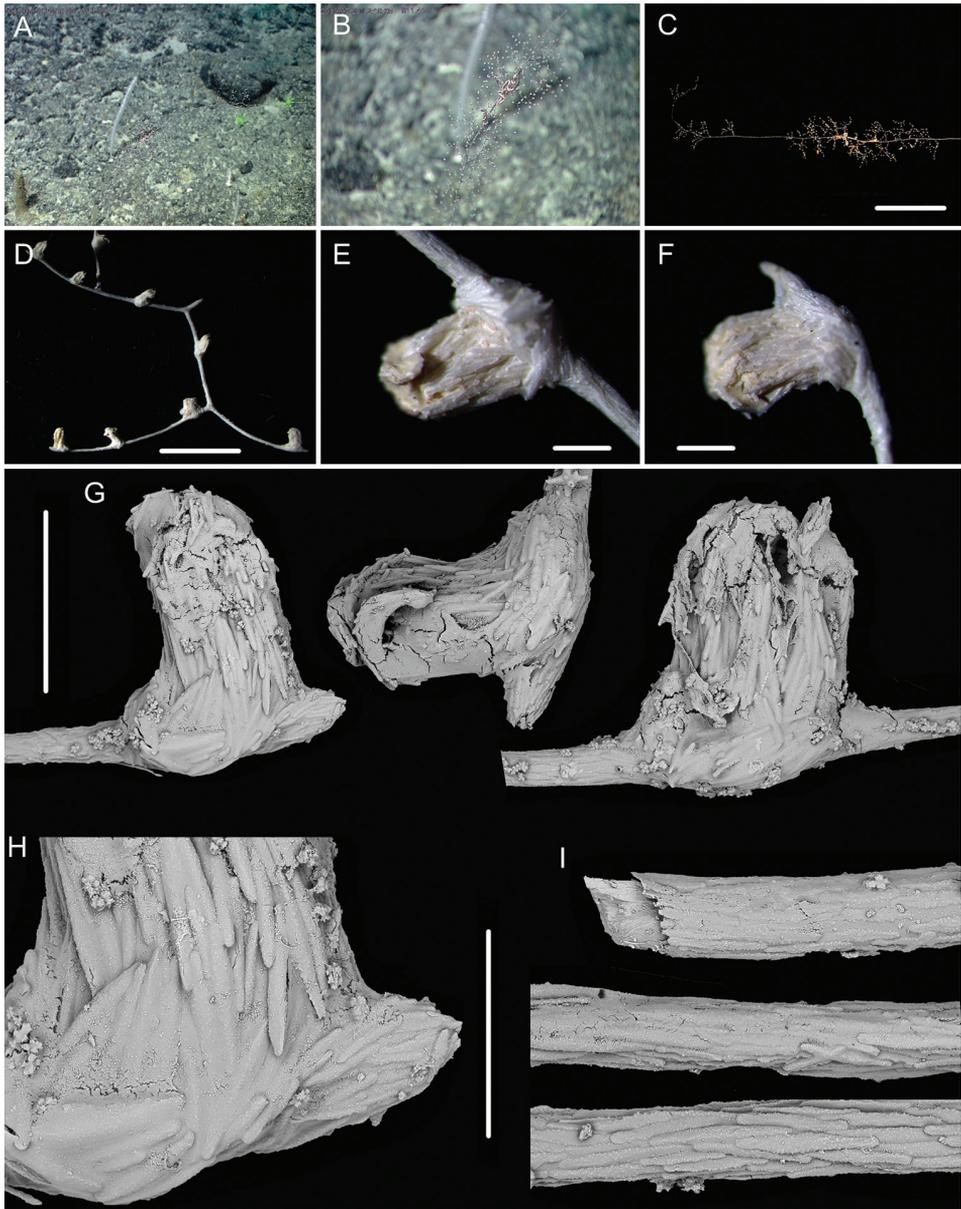
Figures 11–18; Tables 2, 3

*Metallogorgia macrospina* Kükenthal, 1919: 504–505, figs 227–229, Taf.XXX, Fig. 6.

**Type locality.** 0°58.2'S, 90°43.2'E, West Sumatra, 1280 m depth (Kükenthal 1919).

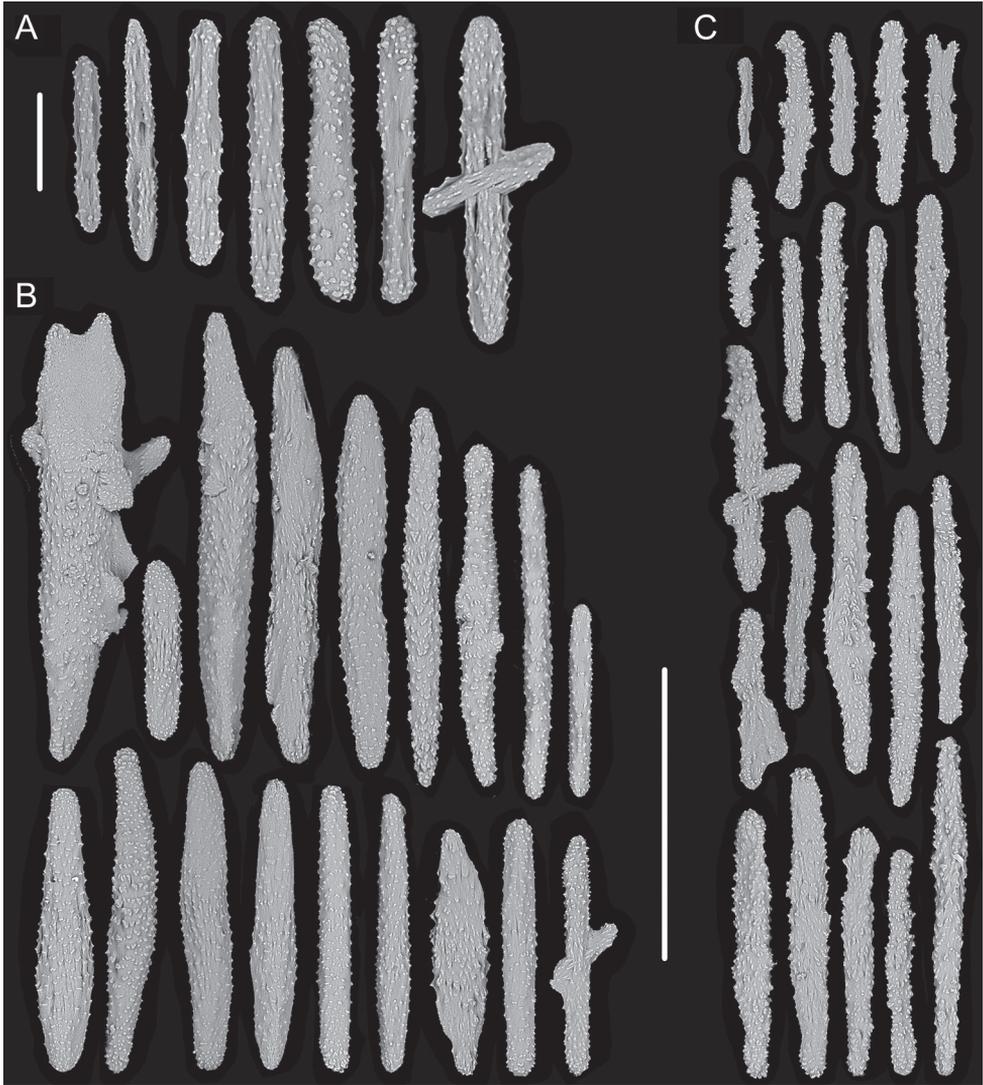
**Voucher specimens.** MBM286484, station FX-Dive 210 (10°04.68'N, 140°12.07'E), depth 911 m, 28 May 2019. MBM286487, station FX-Dive 215 (10°04.97'N, 140°10.75'E), depth 986 m, 2 June 2019. MBM286488, station FX-Dive 215 (10°04.82'N, 140°10.90'E), depth 902 m, 2 June 2019. MBM286489, station FX-Dive 223 (10°04.63'N, 140°15.12'E), depth 1072 m, 11 June 2019. They were collected from three seamounts (tentatively named as M5, M7 and M8) located on the Caroline Ridge.

**Diagnosis (extended on the basis of Kükenthal 1919).** In adults, main stem monopodial with branches forming a similar spiral on the top. Strong branches subdivided dichotomously, with branchlets forming a sympodium pattern in each plane. In juveniles, main stem monopodial and thin/gracile with branches occurring on the lateral of the trunk randomly and subdivided dichotomously in mul-



**Figure 11.** External morphology and polyps of juvenile *Metallogorgia macrospina* MBM286484 **A** the colony *in situ*. Laser dots spaced at 33 cm used for scale **B** close-up of branches *in situ* **C** the colony after collection **D** a branch under a light microscope **E, F** a single polyp under a light microscope **G** three polyps under SEM **H** polyp-body wall under SEM **I** coenenchyme under SEM. Scale bars: 10 cm (**C**), 5 mm (**D**), 1 mm (**G**), and 500  $\mu$ m (**E, F, H, I; H, I** at the same scale).

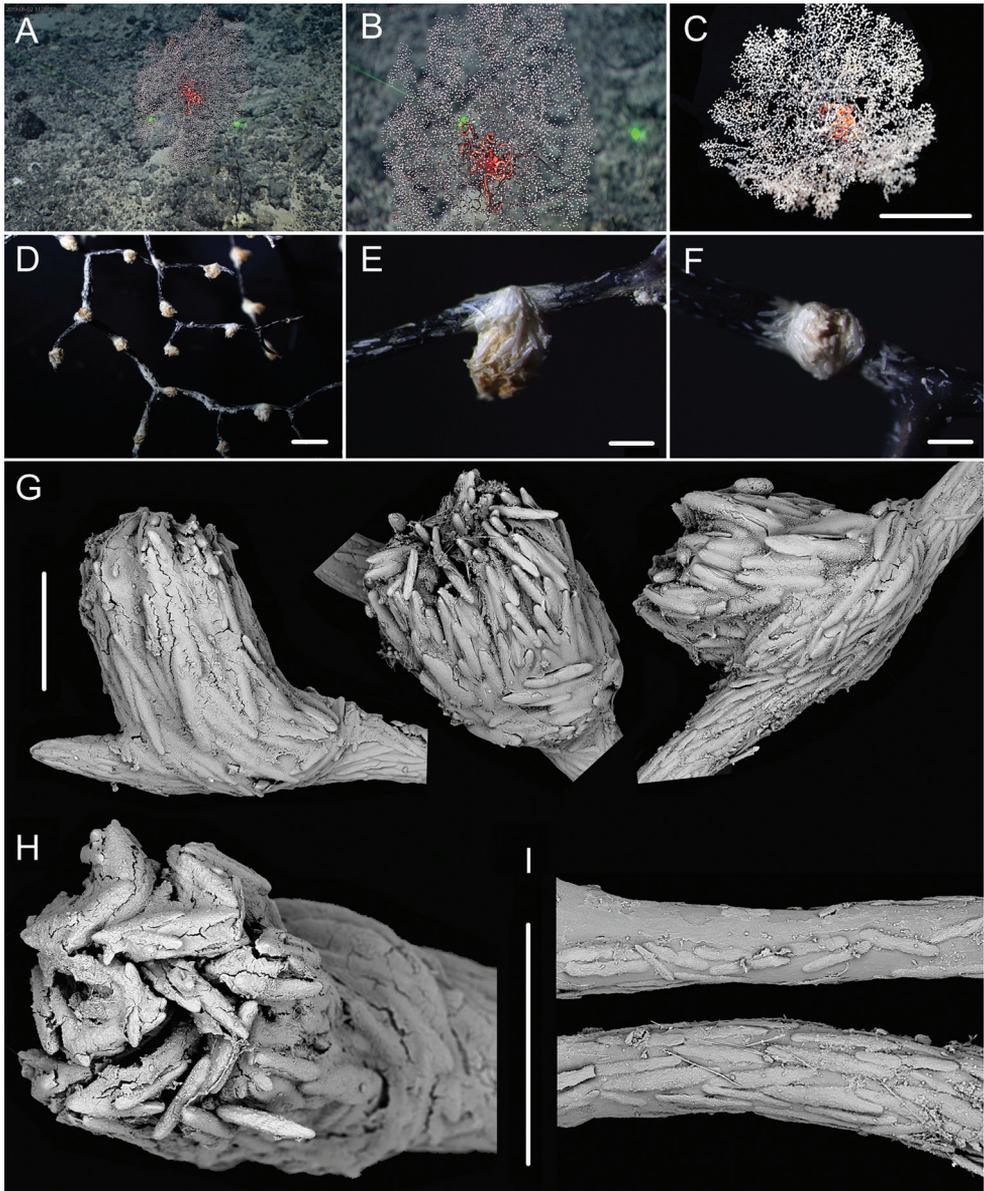
tiple planes. Polyp cylindrical, some of them with a slightly expanded base, absent on stem of adults but present in juveniles. Sclerites relatively coarse with many small warts on surface, cross-shaped occasionally. Rods relatively regular, longitu-



**Figure 12.** Sclerites of juvenile *Metallogorgia macrospina* MBM286484 **A** some small rods in polyps **B** larger rods in polyps **C** rods and elongated scales in coenenchyme. Scale bars: 50  $\mu\text{m}$  (**A**), 300  $\mu\text{m}$  (**B**, **C** at the same scale).

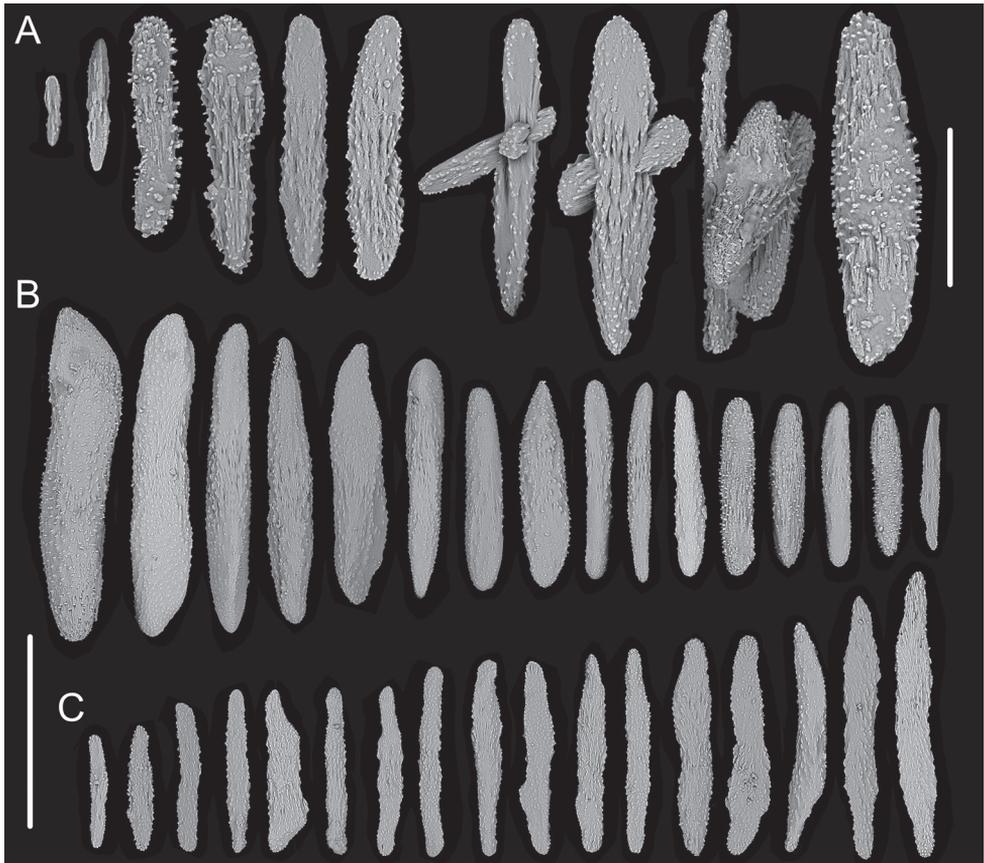
dinally arranged in tentacles and the upper part of the polyp body, and partially crosswise or transversely arranged on the body bottom. Scales and rods elongated, usually coarse with serrated edges, transversely arranged in coenenchyme. Nematozooids not present.

**Description.** In juvenile (specimen MBM286484), colony slightly bottlebrush-shaped, with branches occurring on the lateral side of the stem randomly. Main stem monopodial and gracile. Branches subdivided dichotomously in multiple planes. Polyps cylindrical, occasionally present on the top of the stem. The branch coenenchyme



**Figure 13.** External morphology and polyps of *Metallogorgia macrospina* MBM286487 **A** the colony *in situ*. Laser dots spaced at 33 cm used for scale **B** close-up of branches *in situ* **C** the colony after collection **D** a branch under a light microscope **E, F** a single polyp under a light microscope **G** three polyps under SEM **H** head of a polyp under SEM **I** coenenchyme under SEM. Scale bars: 10 cm (**C**), 2 mm (**D**), and 500  $\mu$ m (**E–I**; **H, I** at the same scale).

well differentiated with a layer of sclerites. In the adults (specimen MBM286487–286489), colony like a tree shape with branches forming a similar spiral on the top of the stem. Main stem monopodial and strong. Branches subdivided dichotomously with branchlets forming a sympodium pattern in each plane. Polyps cylindrical, some



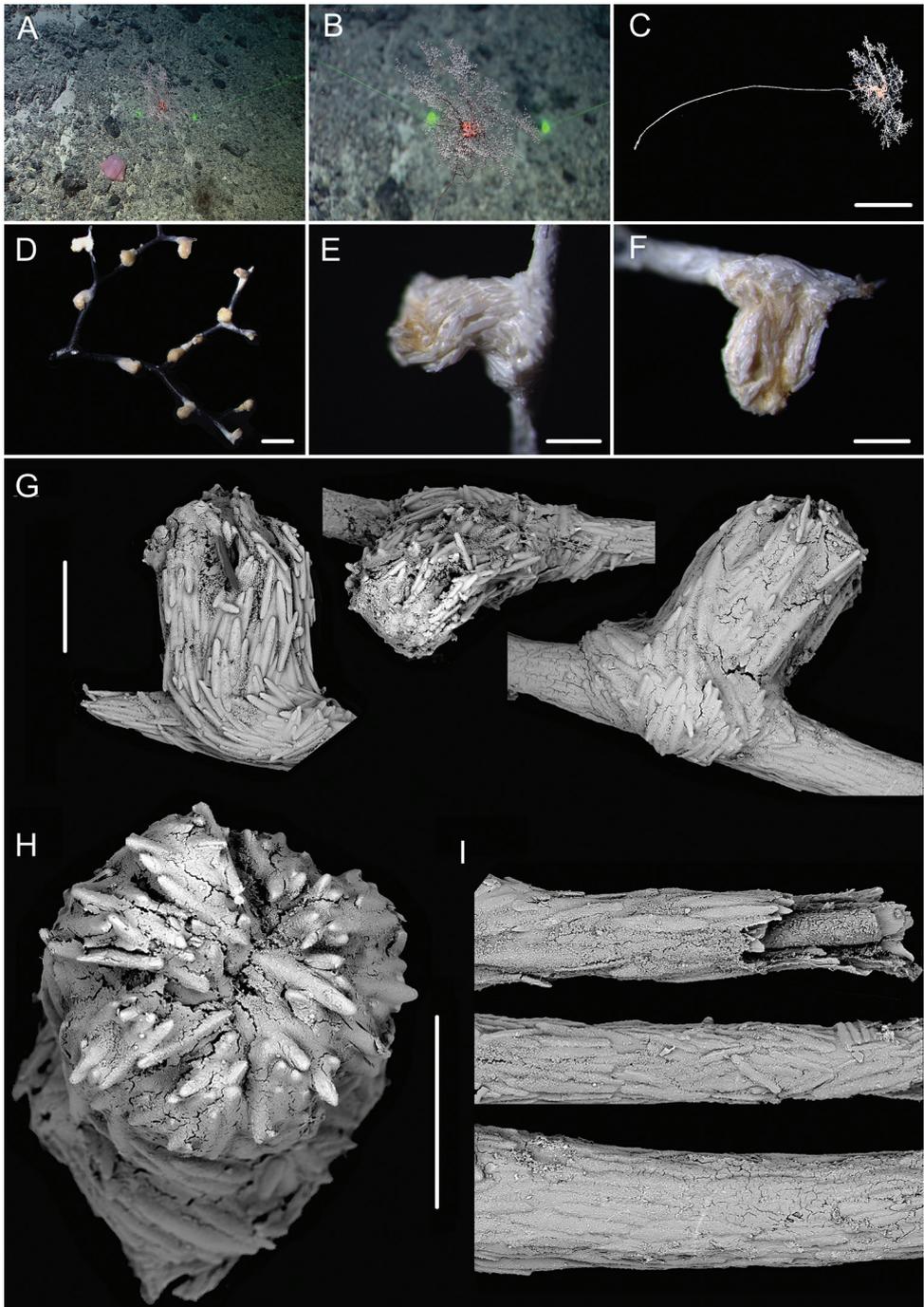
**Figure 14.** Sclerites of *Metallogorgia macrospina* MBM286487 **A** some small rods in polyps **B** larger rods in polyps **C** rods and elongated scales in coenenchyme. Scale bars: 100  $\mu\text{m}$  (**A**), and 300  $\mu\text{m}$  (**B**, **C** at the same scale).

of them with a slightly expanded base, absent from the stem. Branch coenenchyme usually not well differentiated.

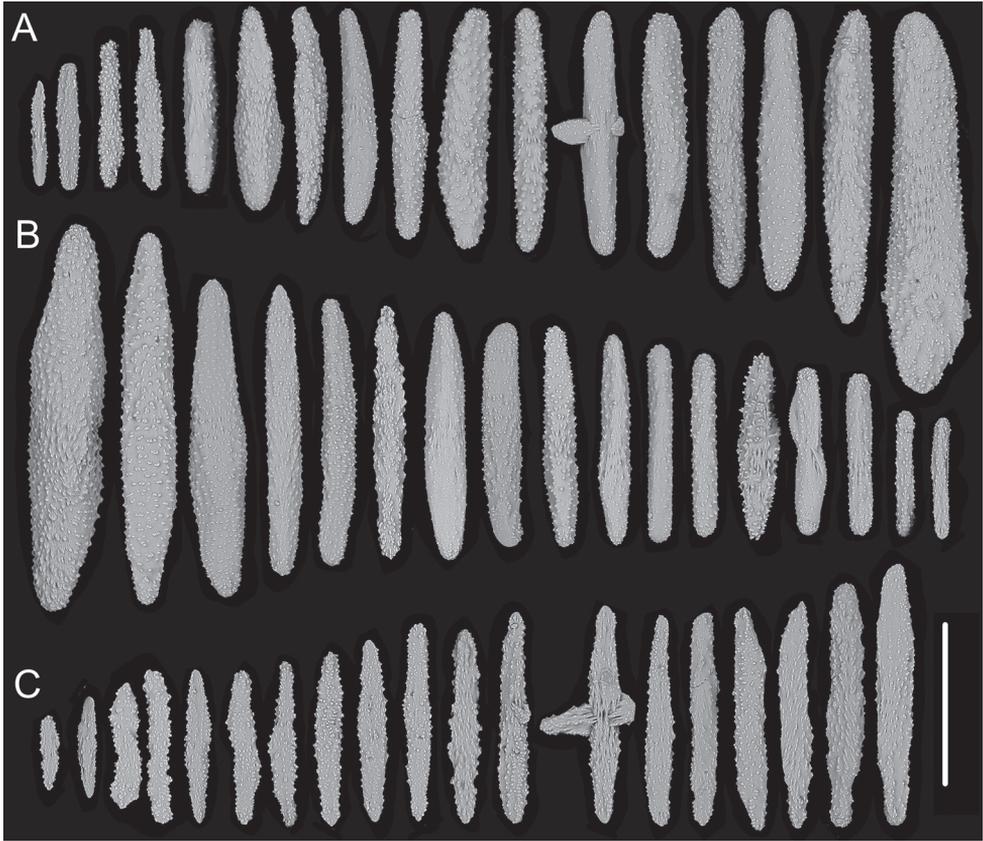
Sclerites with same forms and arrangement in juveniles and adults, both relatively coarse with many small warts on surface, cross-shaped occasionally. Rods relatively regular, longitudinally arranged in tentacles and the upper part of the polyp body, and partially crosswise or transversely arranged on the body bottom. Scales and rods elongated, usually coarse with serrated edges, transversely arranged in coenenchyme. For detailed morphological measurements, see Table 2.

**Distribution.** West Sumatra (Kükenthal 1919); the unnamed seamounts on the Caroline Ridge in the Western Pacific (present study); Southwest Pacific (Pante et al. 2012), 720–1280 m depth.

**Remarks.** According to Kükenthal (1919), the sclerites in the *M. macrospina* polyps contain rods and spindles, and those in coenenchyme are slender rods, some of them flat or irregular. The sclerites in our specimens match well with the original description as well as pictures. Therefore, we identify our specimen as *M. macrospina*.



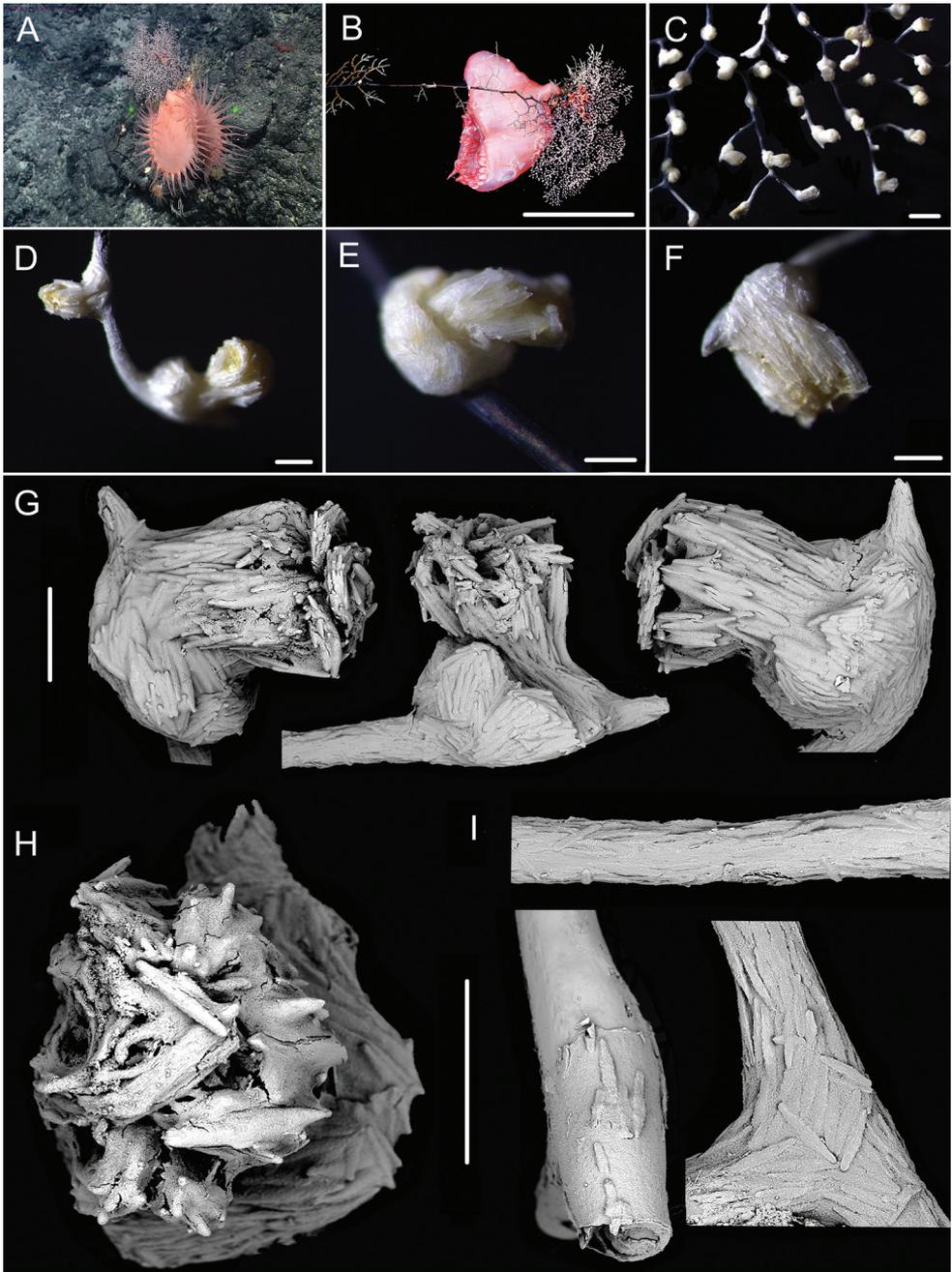
**Figure 15.** External morphology and polyps of *Metallogorgia macrospina* MBM286488 **A** the colony *in situ*. Laser dots spaced at 33 cm used for scale **B** close-up of branches *in situ* **C** the colony after collection **D** a branch under a light microscope **E, F** a single polyp under a light microscope **G** three polyps under SEM **H** head of one polyp under SEM **I** coenenchyme under SEM. Scale bars: 10 cm (**C**); 2 mm (**D**), and 500  $\mu$ m (**E–I**; **H, I** at the same scale).



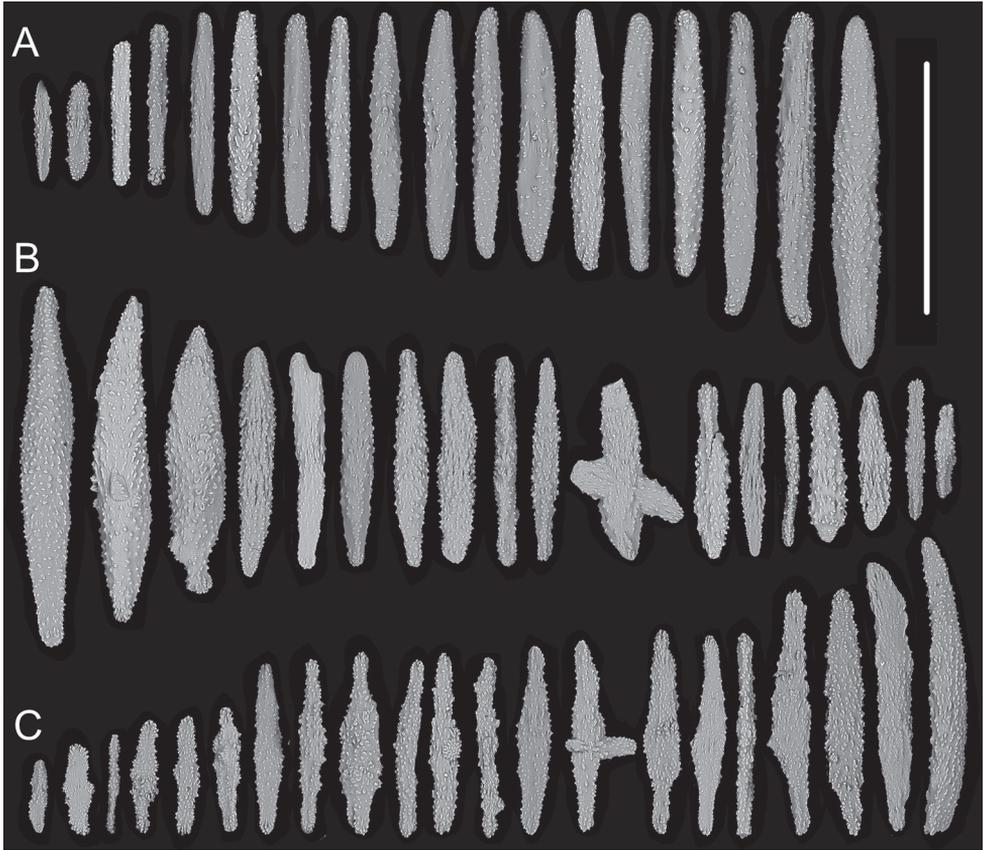
**Figure 16.** Sclerites of *Metallogorgia macrospina* MBM286488 **A** rods in tentacles **B** rods in the polyp-body wall **C** rods and elongated scales in coenenchyme. Scale bar: 200  $\mu\text{m}$  (all images at the same scale).

*Metallogorgia macrospina* is similar to *M. melanotrichos* by the branchlets forming a sympodium pattern in the large branches. In the original description, Kükenthal (1919) pointed out that *M. macrospina* differed from *M. melanotrichos* by its more densely arranged branches, larger polyps, longer sclerites in coenenchyme and different color. However, the polyps of *M. macrospina* in our specimens are generally smaller than those of *M. melanotrichos* (Table 2), and there are no conspicuous differences in color (almost brown to black) among these colonies. Therefore, based on the morphological features of our specimens, *M. macrospina* can be separated from *M. melanotrichos* by its sympodial branching part forming a spiral on the colony top (vs. monopodial), only rods in the polyp-body wall (vs. rods and scales), and rods and scales in coenenchyme (vs. only scales).

The juvenile of *Metallogorgia macrospina* (specimen MBM286484) has significant differences in the branching pattern from the adult specimens MBM286487, MBM286488 and MBM286489 in morphology. It differs also by having a slightly bottlebrush-shaped colony (vs. similarly tree-shaped colony), gracile and flexible stem (vs. hard and strong), monopodial branching part (vs. sympodial), branchlets



**Figure 17.** External morphology and polyps of *Metallogorgia macrospina* MBM286489 **A** the colony *in situ*. Laser dots spaced at 33 cm used for scale **B** the colony after collection **C** a branch under a light microscope **D** a terminal branchlet under a light microscope **E, F** a single polyp under a light microscope **G** three polyps under SEM **H** head of one polyp under SEM **I** coenenchyme under SEM. Scale bars: 10 cm (**B**), 2 mm (**C**), and 500  $\mu$ m (**D–I**; **H, I** at the same scale).



**Figure 18.** Sclerites of *Metallogorgia macrospina* MBM286489 **A** rods in tentacles **B** rods in the polyp-body wall **C** rods and elongated scales in coenenchyme. Scale bar: 300  $\mu\text{m}$  (all at the same scale).

in multiple planes (vs. forming a sympodium in one plane), and well differentiated coenenchyme with more sclerites (vs. not well differentiated and with relatively sparse sclerites). However, the same sclerites in polyps and coenenchyme, and particularly the mtMutS gene data analyzed below indicate these specimens belong to the same species.

### Genus *Pseudochrysogorgia* Pante & France, 2010

**Diagnosis (based on Pante and France 2010).** Main stem monopodial or slightly zigzagging with branches subdivided dichotomously in multiple planes, forming a bottlebrush-shaped colony. Most polyps leaning distad and neck narrower than head. Sclerites slightly ornamented, in the form of plates, scales and rods. When polyp not leaning distad, sclerites arranged obliquely on the polyp body. When polyps leaning distad, sclerites mostly arranged longitudinally (parallel to branch) on the polyp body, placed

obliquely in the area of neck, and arranged longitudinally on head and along the back of tentacles. Scales and plates in branch coenenchyme mostly parallel to main branch axis.

**Type species.** *Pseudochrysogorgia bellona* Pante & France, 2010.

**Distribution.** Southwest Pacific (Coral Sea and northeast of New Zealand), 800–1462 m depth (Pante and France 2010, Pante et al. 2012).

### ***Pseudochrysogorgia bellona* Pante & France, 2010**

Figures 19, 20; Table 3

*Pseudochrysogorgia bellona* Pante & France, 2010: 595–612.

**Type locality.** Bellona Plateau, New Caledonia, 800–923 m depth (Pante and France 2010).

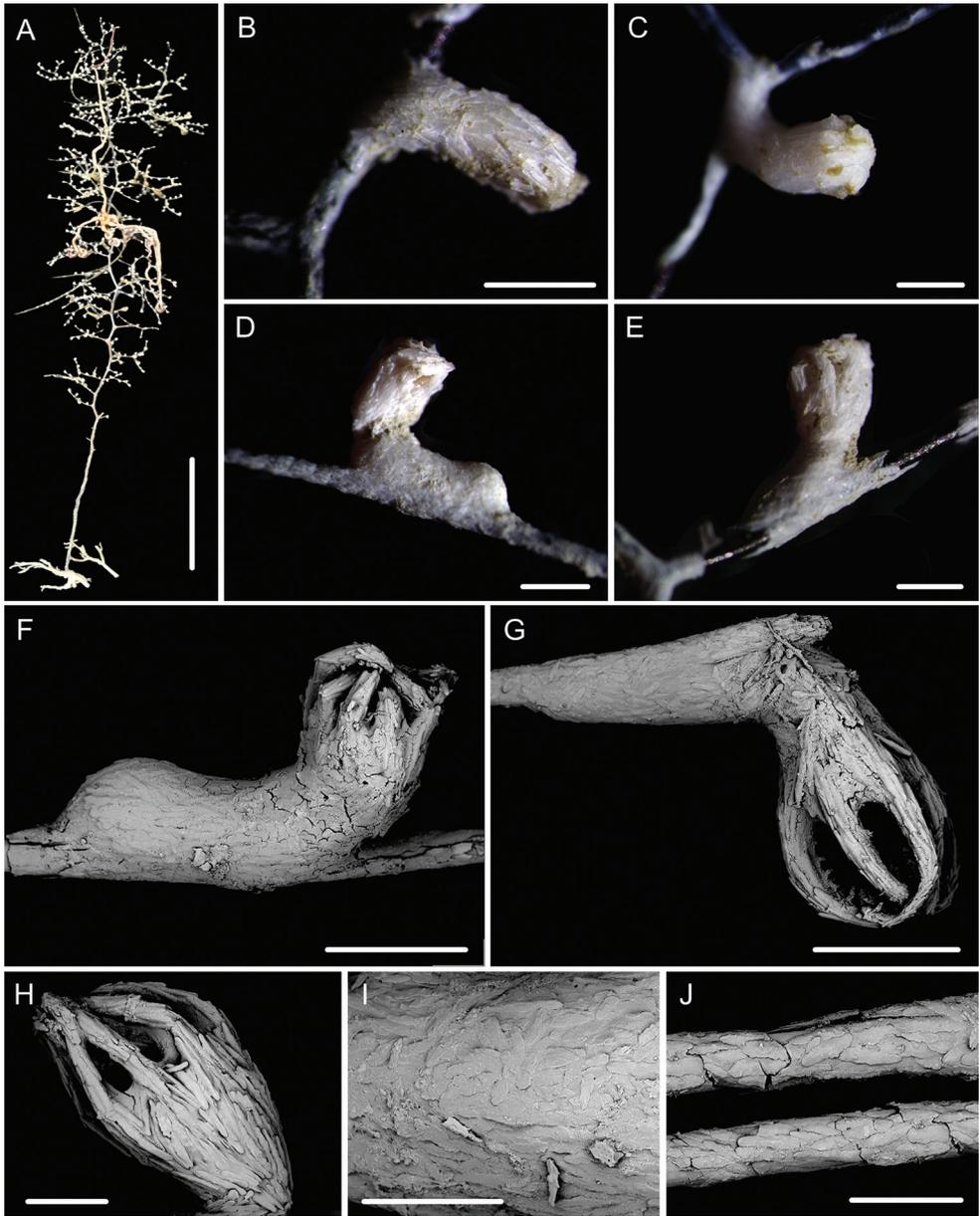
**Voucher specimen.** MBM286490, the Ganquan Plateau in the South China Sea, 586–910 m.

**Description.** No whole colony was obtained, thus the description was based on a picture (Figure 19A) and a few frozen fragments. Colony ca. 50 cm long and 11 cm wide with dendritic holdfast ca. 12 cm long. Main stem more zigzagging. Branching sequences unknown. Branches subdivided dichotomously, up to sixth order with distance between adjacent branches 10–25 mm. Polyps cylindrical, or with an expanded body base and obviously narrow neck, 1.0–2.5 mm long and 0.5–2.5 mm wide at bases, with tentacles up to 1 mm long (Figure 19B–G).

Rods with many small warts on surface, usually with two round ends and relatively less ornamentation, longitudinally arranged along the back of tentacles, and measuring  $142\text{--}598 \times 11\text{--}84 \mu\text{m}$  (Figures 19H, 20A). Sclerites in the polyp-body wall including rods, usually with one sharp end, and scales, slightly ornamented, some of them thick and elongated, and measuring  $150\text{--}620 \times 31\text{--}127 \mu\text{m}$ . When the polyp not leaning distad, rods and elongated scales arranged obliquely in the polyp-body wall. While polyps leaning distad, scales mostly arranged longitudinally (parallel to the branch) in upper of body, rods and scales placed obliquely in neck region, and arranged longitudinally on head and the base of tentacles (Figures 19I, 20B). Scales slightly ornamented, mostly parallel to main branch axis in coenenchyme, and measuring  $115\text{--}397 \times 16\text{--}150 \mu\text{m}$  (Figures 19J, 20C).

**Distribution.** Bellona Plateau, Coral Sea and Otara Seamount, at southern tip of the Kermadec Ridge (Pante and France 2010, Pante et al. 2012); and South China Sea (present study), 586–1462 m depth.

**Remarks.** *Pseudochrysogorgia bellona* Pante & France, 2010 resembles the species of *Chrysogorgia* Duchassaing & Michelotti, 1864 by having dichotomously subdivided branches arising from the main stem in a spiraling fashion and forming a bottlebrush-shaped colony. However, it differs in the monopodial or more zigzagging stem (vs. almost sympodial, except *Chrysogorgia abludo* Pante & Watling, 2012 and *C. dendritica* Xu, Zhan & Xu, 2020) and obviously different polyps (Xu et al. 2020).



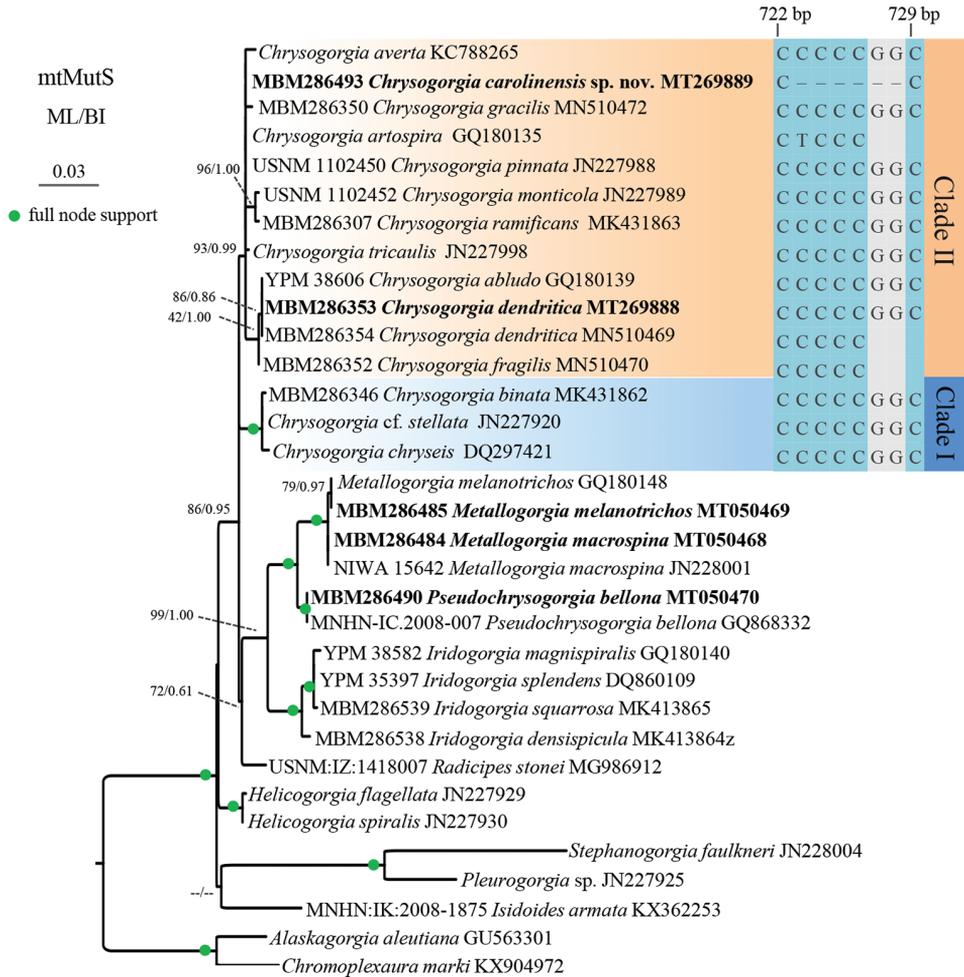
**Figure 19.** External morphology and polyps of *Pseudochrysogorgia bellona* **A** the colony after collection **B–E** a single polyp under a light microscope **F, G** a single polyp under SEM **H** head of one polyp under SEM **I** basal polyp body under SEM **J** coenenchyme under SEM. Scale bars: 10 cm (**A**), 1 mm (**B–G**), and 500  $\mu$ m (**H–J**).

Furthermore, *P. bellona* is similar to species of *Metallogorgia* Versluys, 1902 in its monopodial colony and has a close genetic distance as well. However, *P. bellona* can be separated by its polyps usually with obviously narrow neck (vs. none), dendritic



**Figure 20.** Sclerites of *Pseudochrysogorgia bellona* **A** rods in tentacles **B** rods and scales in the polyp-body wall **C** scales in coenenchyme. Scale bar: 300  $\mu\text{m}$  (all images at the same scale).

holdfast (vs. discoid) and sclerites including plates, scales and rods with more ornamentation (vs. almost rods and scales with little ornamentation) (Pante and France 2010). In our specimen, the rods in tentacles are more regular usually with two round ends and less ornamentation. The elongated thick scales are more abundant in coenenchyme, and plates are scarcer than the type colony. We suggest that these differences are population-dependent.



**Figure 21.** Maximum likelihood (ML) tree inferred from the mtMutS sequences of *Chrysogorgia*, *Metallogorgia*, *Pseudochrysogorgia* and related species. Numbers at the nodes represent the ML bootstrap values and the posterior probability values of Bayesian analysis (BI). Newly sequenced species are in bold. Support  $\leq 50\%/0.50$  is shown as ‘--’. Alignment flatfile showed the mtMutS deletion for *Chrysogorgia carolinensis* sp. nov. with “-”, using *C. averata* KC788265 as a reference.

## Molecular sequences, genetic distances, and phylogenetic analyses

The conspecific sequences for each newly sampled species were identical, and only the holotype sequence was deposited in GenBank and analysed here. The accession number and the length are as follows: MT269889, 686 bp for *Chrysogorgia carolinensis* sp. nov., MT269888, 693 bp for *C. dendritica*, MT050468, 691 bp for *M. macrospina*; MT050469, 695 bp for *M. melanotrichos*, MT050470, 690 bp for *P. bellona*. The alignment dataset comprised 629 nucleotide positions. Compared to the other *Chrysogorgia* species, *C. carolinensis* sp. nov. has six-nucleotide deletion in the mtMutS sequence (Figure 21). There was no intraspecific variability, while the interspecific dis-

tances ranged from zero to 2.42% (Table 4). The genetic distances between the new species *C. carolinensis* sp. nov. and its congeners were in range of 0–2.42%, and those between *C. dendritica* and its congeners were in the range of 0–1.63%. To date, only three species are available for the genetic distance and phylogenetic analysis for *Metallogorgia* and *Pseudochrysogorgia*. The mtMutS genetic distances between *M. macrospina* and *M. melanotrichos* was 0.16%, while there was no intraspecific variation within the two species and *P. bellona* (Table 4). The genetic distances between *Metallogorgia* and *Pseudochrysogorgia* were 1.94% and 2.10%.

The ML and BI phylogenetic trees are identical in topology, and thus only the former with the both support values is shown (Figure 21). In both trees, *Metallogorgia*, *Pseudochrysogorgia*, *Iridogorgia*, *Radicipes* and *Chrysogorgia* formed a “monophyletic Chrysogorgiidae clade” (MCC) sensu Pante et al. (2012) with moderate to high support (ML 86%; BI 0.95). The *Chrysogorgia* species were separated into two main clades (Clade I and II) with high support values, which is consistent with Xu et al. (2019, 2020). Clade I includes the sister species *C. binata*, *C. cf. stellata* and *C. chryseis*, and Clade II contains all the rest species. The species *C. dendritica* and *C. abludo* formed a sister subclade, followed by *C. fragilis*. *Chrysogorgia carolinensis* sp. nov. formed a sister subclade with the cluster *C. ramificans* + *C. monticola*, the group *C. dendritica* + *C. abludo* + *C. fragilis* and the rest species within Clade II. *Metallogorgia melanotrichos* and *M. macrospina* formed sister clade, followed by *P. bellona* with full node support (Figure 21).

## Discussion

Both the morphology and molecular phylogenetic analysis support the assignment of the new species to the genus *Chrysogorgia* Duchassaing & Michelotti, 1864. The barcoding analysis of mtMutS is considered as the first step in molecular identification of octocorals (McFadden et al. 2011; Pante et al. 2012). However, the mtMutS genetic distances within *Chrysogorgia* are relatively low, and there is no barcoding gap (intraspecific zero vs. interspecific 0–2.42%) for species identification, as shown by Xu et al. (2020). Thus, the discrimination of the closely related species was mainly relied on other molecular evidence and morphological characters. Alternatively, single mutations on mtMutS can be used to separate *Chrysogorgia* species (Pante and Watling 2012; Pante et al. 2015; Xu et al. 2020). The mtMutS sequence of *C. carolinensis* sp. nov. has six deletion mutations compared to those of its congeners (Figure 20), supporting the establishment of the new species. Furthermore, the closely related species *C. carolinensis* sp. nov., *C. artospira* and *C. pinnata* are easily separated by the 1/3L branching sequence (vs. 2/5L and flabellate, respectively) and amoeba-shaped scales at the basal polyp body (vs. regular scales and rods, respectively) (Cairns 2007; Pante and Watling 2012). No genetic variability was observed between *C. dendritica* and the closely related species *C. abludo*. However, the former is morphologically distinctly different from the latter by the presence of irregular sclerites in the polyp-body wall

**Table 4.** The uncorrected pairwise distances at mtMutS between *Chrysgorgia*, *Metallogorgia*, and *Pseudochrysgorgia* species/populations.

|    | 1   | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    | 13    | 14    | 15    | 16    | 17 |  |
|----|---|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|----|--|
| 1  | <i>C. abuldo</i> GQ180139, JN227999   | 0     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |    |  |
| 2  | <i>C. dendritica</i> MN510469, <b>MT269888</b>  | –     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |    |  |
| 3  | <i>C. fragilis</i> MN510470   | 0.16% | 0.16% | –     |       |       |       |       |       |       |       |       |       |       |       |       |    |  |
| 4  | <i>C. gracilis</i> MN510472   | 0.97% | 0.97% | 1.13% | –     |       |       |       |       |       |       |       |       |       |       |       |    |  |
| 5  | <i>C. evrolinensis</i> sp. nov. <b>MT269889</b>   | 0.81% | 0.81% | 0.65% | 0.33% | –     |       |       |       |       |       |       |       |       |       |       |    |  |
| 6  | <i>C. arthropina</i> GQ180132–GQ180135, GQ353317  | 0.81% | 0.81% | 0.65% | 0.48% | 0     | 0     | –     |       |       |       |       |       |       |       |       |    |  |
| 7  | <i>C. primata</i> JN227988  | 0.81% | 0.81% | 0.65% | 0.48% | 0     | 0     | –     |       |       |       |       |       |       |       |       |    |  |
| 8  | <i>C. tricaulis</i> JN227998, JN227990, JN227991, GQ180123–GQ180131, EU268056   | 0.97% | 0.97% | 0.81% | 0.65% | 0.16% | 0.16% | 0     | 0     | –     |       |       |       |       |       |       |    |  |
| 9  | <i>C. avenata</i> KC788265, GQ180136  | 1.13% | 1.13% | 0.97% | 0.81% | 0.33% | 0.32% | 0.32% | 0.48% | 0     |       |       |       |       |       |       |    |  |
| 10 | <i>C. monticola</i> JN227989  | 1.45% | 1.45% | 1.29% | 1.13% | 0.65% | 0.65% | 0.65% | 0.81% | 0.97% | –     |       |       |       |       |       |    |  |
| 11 | <i>C. namificans</i> MK431863   | 1.45% | 1.45% | 1.29% | 1.13% | 0.65% | 0.65% | 0.65% | 0.81% | 0.97% | 0.32% | –     |       |       |       |       |    |  |
| 12 | <i>C. chryseis</i> JN227992, DQ297421   | 2.42% | 2.42% | 2.26% | 2.10% | 1.63% | 1.62% | 1.62% | 1.78% | 1.94% | 2.26% | 2.26% | –     |       |       |       |    |  |
| 13 | <i>C. binata</i> MK431862   | 2.42% | 2.42% | 2.26% | 2.10% | 1.63% | 1.62% | 1.62% | 1.78% | 1.94% | 2.26% | 2.26% | 0.48% | –     |       |       |    |  |
| 14 | <i>C. cf. stellata</i> JN227920   | 2.26% | 2.26% | 2.10% | 1.94% | 1.46% | 1.45% | 1.62% | 1.78% | 2.10% | 2.10% | 0.32% | 0.16% | –     |       |       |    |  |
| 15 | <i>Metallogorgia macrospina</i> <b>MT050468</b> , JN228001, JN227906  | 5.33% | 5.33% | 5.17% | 4.85% | 4.55% | 4.52% | 4.68% | 4.52% | 5.17% | 5.17% | 5.17% | 5.01% | 0     | –     |       |    |  |
| 16 | <i>M. melanotricha</i> <b>MT050469</b> , GQ868333, GQ868339, GQ868340, GQ180146–GQ180155, GQ180156–GQ180158, GQ180162, GQ180163, GQ353314, EU268057, DQ297423 | 5.49% | 5.49% | 5.33% | 5.01% | 4.72% | 4.68% | 4.68% | 4.85% | 4.68% | 5.33% | 5.33% | 5.33% | 5.17% | 0.16% | 0     |    |  |
| 17 | <i>Pseudochrysgorgia bellona</i> <b>MT050470</b> , GQ868331, GQ868332   | 4.04% | 4.04% | 3.88% | 3.55% | 3.25% | 3.23% | 3.39% | 3.55% | 3.88% | 3.88% | 4.52% | 4.52% | 4.36% | 1.94% | 2.10% | 0  |  |



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# A new species of *Pseudosinella* Schäffer, 1897 (Collembola, Entomobryidae) from Altamira Caves (Cantabria, Spain)

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## Abstract

This paper describes *Pseudosinella altamirensis* sp. nov. from the Altamira Caves, municipal district of Santillana del Mar (Cantabria, Spain), and five other caves near the coast of Cantabria (northern Spain). Its taxonomic position is discussed and differences and similarities among morphologically and geographically close species are highlighted. The new species can be identified by its five eyes, the basal and small inner paired teeth on the claw, and the length of the uncrenulated part of the distal dens.

## Keywords

cave dwelling fauna, chaetotaxy, northern Spain, *Pseudosinella altamirensis* sp. nov., taxonomy

## Introduction

During sampling work to increase the knowledge of the Collembolan cave fauna of the Cantabrian Mountains, we have captured a considerable number of undescribed species of Collembola. Some of these, mainly *Pseudosinella* Schäffer, 1897, are new species, and it is necessary to describe them. In this paper, a new species of the genus *Pseudosinella*

is described, found in some limestone caves within the municipal districts of Miengo, Santillana del Mar, Reocín, and Cabuérniga (Fig. 1). A complete review of specimens collected in Altamira and other nearby caves (see Luque and Labrada 2016 for details) has shown that this new species was erroneously attributed to *Pseudosinella superoculata* Gisin & Gama, 1969 by Luque and Labrada. Dorsal macrochaetotaxy and other morphological characters have been used here for species identification. Christiansen et al. (1983) produced a catalogue of world *Pseudosinella* species and established a code for dorsal macrochaetotaxy characters. Christiansen et al. (1990) designed a computer-assisted identification key (Delta key) of the species of *Pseudosinella* with more characters. This electronic key is now available on the Web and regularly updated (Jordana et al. 2020). The new species was easily detected using this electronic key by the combination of chaetotaxy formula and other characters used in *Pseudosinella* species description.

## Materials and methods

### Abbreviations used in the description and figures:

|               |  |
|---------------|--|
| <b>Abd</b>    | abdominal tergite                        |
| <b>accp</b>   | accessorial p-sensilla                   |
| <b>Ant</b>    | antennal segment                         |
| <b>a.s.l.</b> | above sea level                          |
| <b>Mc</b>     | macrochaeta(e)                           |
| <b>mes</b>    | mesochaeta(e)                            |
| <b>mic</b>    | microchaeta(e)                           |
| <b>MZNA</b>   | Museum of Zoology, University of Navarra |
| <b>pse</b>    | pseudopore                               |
| <b>Th</b>     | thoracic tergite                         |

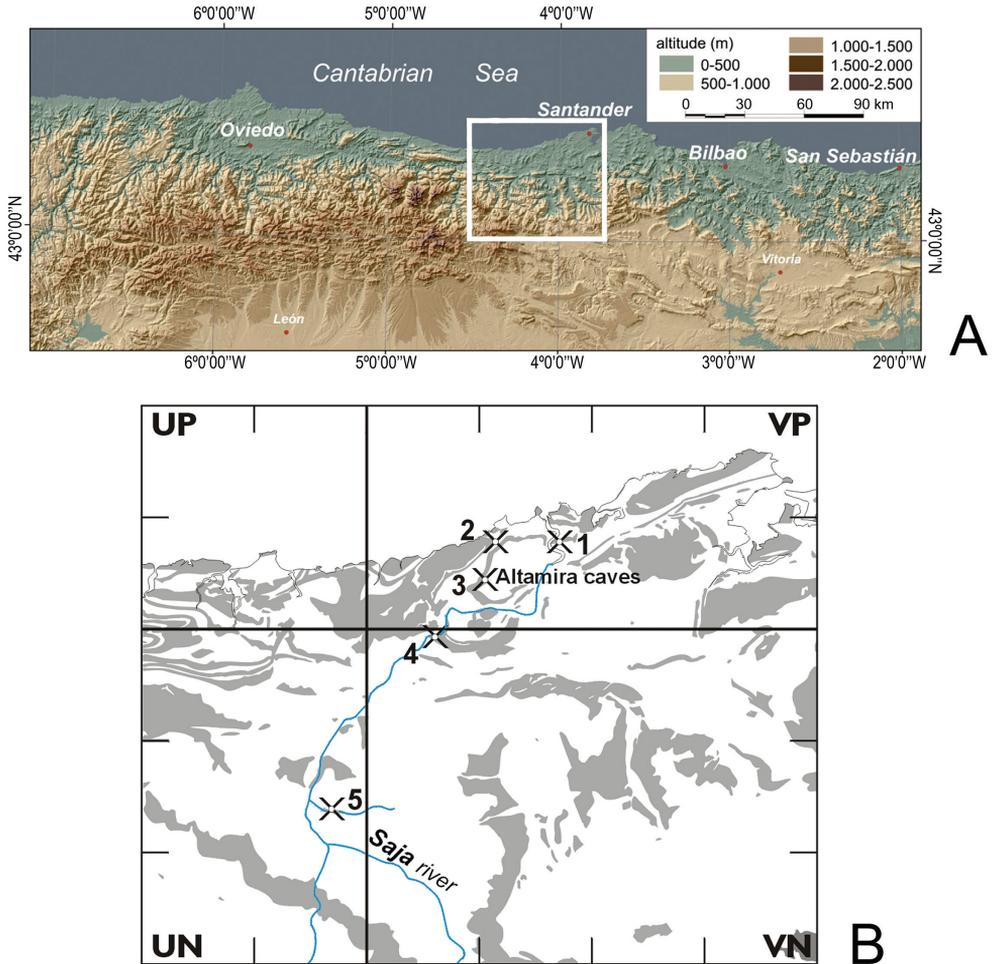
### Terminology

Dorsal head and body chaetotaxy follows Gisin (1965, 1967a, b), Szeptycki (1979), and Soto-Adames (2010). Equivalence between the notation proposed by Gisin and the AMS system *sensu* Soto-Adames 2010 is given in Table 1.

The characters defined by Christiansen et al. (1990) for *Pseudosinella* and those used by Christiansen (2013) and Jordana et al. (2020) in the Delta key have been used for identification. Some characters proposed by Mateos (2008) and Winkler and Mateos (2018) have also been considered.

### Study area

The Saja River catchment is in the central sector of the Cantabrian mountain range and flows to the Cantabrian Sea after following a course of 67 km in which it descends approximately 1700 m in altitude. It follows a practically rectilinear south-north course



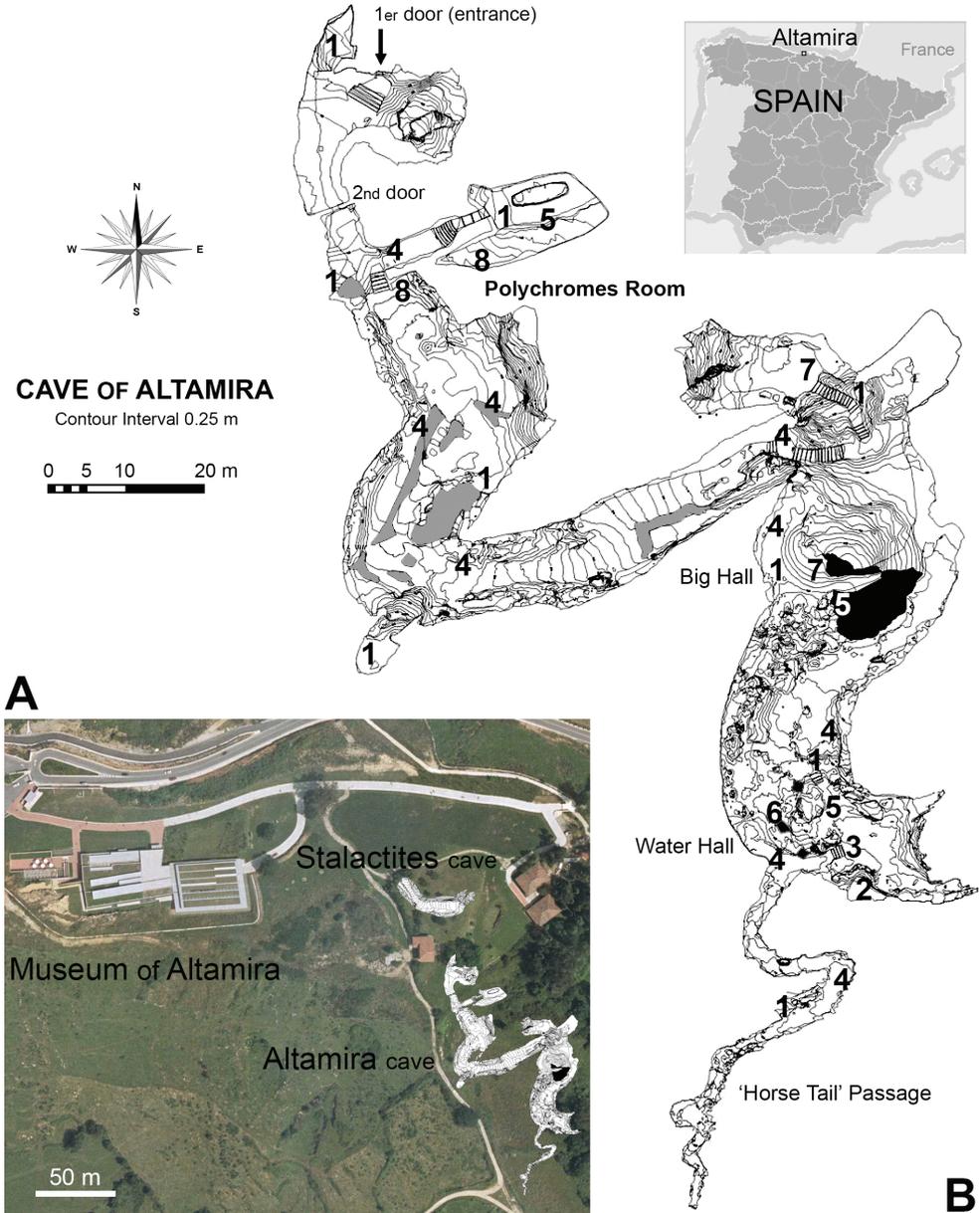
**Figure 1.** Location of the studied area. **A** Cantabrian Mountains (northern Spain) **B** UTM grid map with 10 km squares of the central region of the Cantabrian Mountain to show the outcrops of the rock systems (in grey) which contain limestone and geographical situation of the study area with the distribution of the cave-dwelling *Pseudosinella altamirensis* sp. nov.: (1) Cudón cave; (2) La Venta del Cuco cave; (3) Altamira and Stalactites caves; (4) Peña Caranceja cave; (5) Cobezo cave. Source: Spanish Geological Institute and Cartographic Service of the Cantabrian Government, scale 1:50 000.

in its middle and upper sections, and in its lower one it flows in a west-east direction, which changes to a south-north direction in its final reach at the mouth of the San Martín de la Arena estuary between the municipalities of Miengo and Suances (Fig. 1). This course coincides with the main fracturing and folding lines which characterise the area. In the two municipalities which compose the middle course (Ruento and Cabuérniga), a dismantling of Cretaceous sandstones and clays has taken place, promoting the rising to the surface of Jurassic carbonate materials (Fig. 1). Among the few cavities known over these Jurassic limestones are the caves of Poyo and Cobezo (also the caves located in the Saja-Besaya Natural Park) and the flooded Fuentona de Ruento

cave. The first Cretaceous limestone outcrops are in the largest municipalities (Cabezón de la Sal, Reocín, Santillana, and Miengo), which are located along the middle-lower course of the Saja River. In the geologic context, this coastal area is distinguished by the abundance of lower to upper Cretaceous carbonates, which favours karst development. Among the abundant explored cavities in these limestone rocks are two (the caves of Peña Caranceja and La Venta del Cuco) that harbor the new species described here. Cudón cave, which has prehistoric paintings, is near the town of the same name at the opening of the Saja River that forms the San Martín de la Arena estuary; Cudón cave is approximately 9 km from Altamira Cave (Fig. 1).

The Altamira Cave is in the central region of Cantabria (northern Spain), in one of the limestone hills that surround the small valley in Santillana village. On the whole, the geological and structural characterisation of Altamira Cave (270 m in length) indicates the evolution of a karstic complex from the first prehistoric human occupation until present. It is one of the many caves in the upper vadose area of the tabular polygenic karstic system that developed on Cretaceous calcarenite limestones (Sánchez et al. 2007). This area is known as Santa Olaja, although it is also known by the name of Planes (Santillana del Mar), where the medieval chronicles place the site of the “Sant[a] Illana” monastery (Luque and Labrada 2016). The small plain that extends over the Altamira Cave has an elevated position (159 m a.s.l.) below the Mount Santa Olaja hill range (168 m a.s.l.), and is protected between the mounts of Vispieres (226 m a.s.l.) and Cildad (287 m a.s.l.). This area separates the Saja River catchment from the Santillana physiographic basin (66 m a.s.l.). Altamira Cave, lying 4 km from the sea, is little more than 2 km from the nearby Saja River. It is situated on a topographical high point (152 m a.s.l.) and is only 3–22 m (averaging 8 m) below the surface. Having a length of 270 m, the cave features a main passage 2–12 m high, and 6–20 m wide (Fig. 2). It was discovered in 1868; exploration began in 1875, but it was not until 1879 when the first paintings, one of the first to be cataloged as Palaeolithic, were discovered by Marcelino Sanz de Sautuola (Lasheras 2009). Regarding the cave biology, Ignacio Bolívar was the first entomologist to explore the Altamira Cave in July 1883 (Luque and Labrada 2014, 2016). Since then, entomological visits to the cave have been rather sporadic. For example, in the early 20<sup>th</sup> century, Charles Alluaud (28 June 1913) and Cándido Bolívar (28 August 1915) explored this cave (Luque and Labrada 2014, 2016). On 7 May 1924, the cave and its surrounding area was protected by a resolution of the Government of Spain. Since 1985, the cave and its paintings have been included in the UNESCO list of World Heritage Sites (SC-85/Conf. 008/9 1985).

Furthermore, a small cave with stalactites was discovered in the summer of 1928 when stone was being quarried out for the construction of a road to Altamira Cave. It is purely of geological interest, with beautiful stalactites and stalagmites, as no cave art has been found within. In October 1935, Hans Jürgen Stammer was the first entomologist that explored the Stalactites Cave (Luque and Labrada 2016). This cave also hosts the new species described here.



**Figure 2.** Geographical location of Altamira Caves (Cantabria, Spain). **A** location and ground plan of the Altamira Caves and its museum **B** location of the *Pseudosinella altamirensis* sp. nov. sampling sites along Altamira Cave (August 2000): (1) areas where soil contained mouldy rat or bat faeces; (2) areas where soil contained a rat cadaver (*Rattus rattus*); (3) areas where soil contained a bat cadaver (*Rhinolophus hiposideros*); (4) areas where walls had insect cadavers with visible fungal; (5) areas where water drips or flows towards the cave (hygropetric habitats); (6) areas where water had flooded the surface with small rim stone dams or gours; (7) areas with high clay soil content in the water; (8) areas of continuous monitoring of radon. Plan of the caves with its location courtesy of the National Museum and Research Centre of Altamira.

## Specimen collection and measurement

The specimens were obtained by direct capture. Additionally, baited pitfall traps were used in the parts of the cave that were considered favourable for the presence of fauna (Fig. 2) (see Luque and Labrada 2016 for details). The specimens were captured using a manual aspirator and then preserved in vials containing 70% ethyl alcohol. Each vial was labelled with the following data: collection site, coordinates, date of capture, name of the organisation, and person involved in the capture. The specimens were mounted in Hoyer medium, and optical observations were made under an Olympus BX51-TF microscope with a multiviewing system and phase contrast, and an Olympus BX50-F4 microscope with differential interference contrast (DIC). For the measurements, a U-DA drawing attachment UIS (Universal Infinity System) and a scale calibrated with a slide by Graticules Ltd (1 mm divided in 100 parts) was used. For electron microscopy, three specimens were fixed with 4% (v/v) glutaraldehyde in 0.1 M cacodylate buffer (pH 7.3) for 48 h, then stored for 24 h in a 0.25 M sucrose buffer containing 0.1 M cacodylate, and dehydrated using an ethanol series followed by critical-point drying in CO<sub>2</sub>, mounted on aluminium SEM stubs, and coated in Argon atmosphere with 16 nm of gold in an Emitech K550 sputter-coater. SEM observations and photographs were made with a Zeiss DSM940 A.

## Taxonomy

**Class Collembola Lubbock, 1873**

**Order Entomobryomorpha Börner, 1913**

**Family Entomobryidae Schäffer, 1896**

**Subfamilia Lepidocyrtinae Wahlgren, 1906**

**Genus *Pseudosinella* Schäffer, 1897**

***Pseudosinella altamirensis* sp. nov.**

<http://zoobank.org/2f1163c5-c7d2-43e7-93a7-b7d30c2f11d0>

Figs 3–7

**Type material. *Holotype*:** SPAIN • ♀; Cantabria, municipal district of Santillana del Mar, **Altamira Cave**, Sala de Polícromos (Polychromes Room), National Museum and Research Centre of Altamira; 43°22.61'N, 4°7.18'W; 148 m a.s.l.; 29 Aug. 2000; C. Glez.-Luque leg.; slide labelled “MZNA-Altamira 6d-01”. ***Paratypes*:** • 49 specimens on ethyl alcohol and 3 specimens mounted on SEM stubs; Cueva de las Estalactitas (Stalactites cave); 43°22.64'N, 4°7.21'W; 148 m a.s.l.; 29 Aug. 2000; C. Glez.-Luque leg.; slides MZNA-Altamira 6d-02 to 05 • 3 specimens on slides and 25 in ethyl alcohol; Polychromes Room; 43°22.61'N, 4°7.18'W; 148 m a.s.l.; 24 Mar. 2008; Cesáreo Saiz leg.; slides MZNA-Altamira01-01 and MZNA-Altamira01-02; deposited at the Museum of Zoology, University of Navarra, Pamplona, Spain (MZNA).



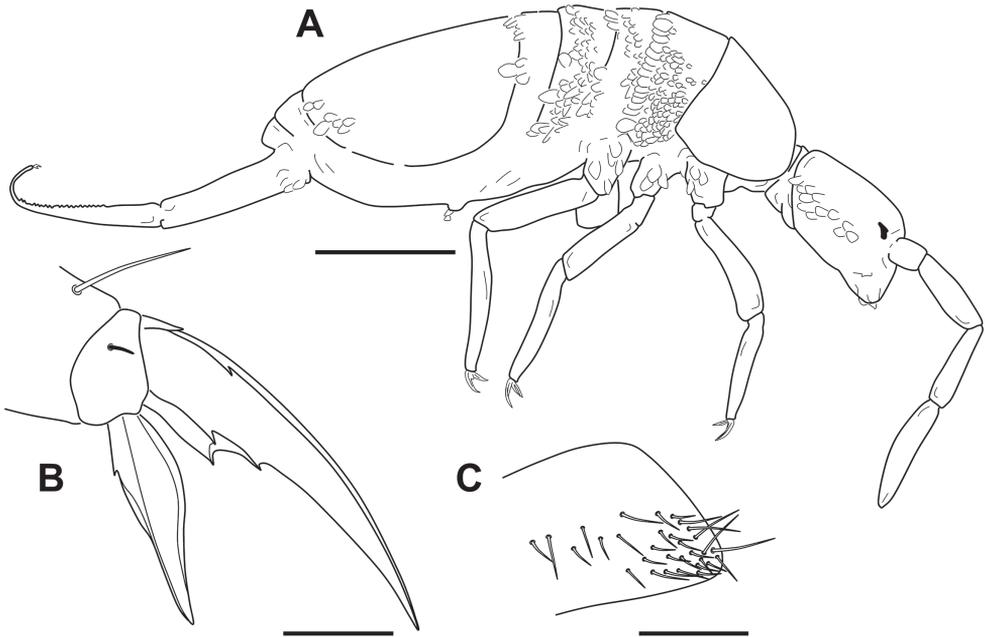
**Figure 3.** *Pseudosinella altamirensis* sp. nov. Habitus. Scale bar: 0.5 mm.

**Other material.** SPAIN – **Cantabria** • 2 specimens on slides and 14 on ethyl alcohol; La Venta del Cuco cave, Ubiarco, Santillana del Mar; 43°24.28'N, 4°6.35'W; 145 m a.s.l.; 13 Sep. 1995; C. Glez.-Luque leg.; slides MZNA-Luque Coll. 13d-01 and 02 • 1 specimen on slide and 1 in ethyl alcohol; Cudón cave, Cudón, Miengo; 43°24.94'N, 4°0.74'W; 22 m a.s.l.; 14 Sep. 1995; C. Glez.-Luque leg.; slide MZNA-Luque Coll. 36d • 1 specimen on slide and 3 in ethyl alcohol; Peña Caranceja or La Peñona cave, Barcenaciones, Reocín; 43°20.33'N, 4°9.45'W; 125 m a.s.l.; 7 Oct. 2000; C. Glez.-Luque leg.; slide MZNA-Luque Coll. 3d • 2 specimens on slide and three in ethyl alcohol; Cobezo, Cobeján or Perro cave, Viaña, Cabuérniga; 43°11.61'N, 4°16.52'W; 360 m a.s.l.; 15 Jun. 1996; C. Glez.-Luque leg.; slide MZNA-Luque Coll. 7d.

**Diagnosis.** 5 + 5 ocelli. Antennae moderately long. Ant III sense organ with two paddle- or leaf-shaped and two additional sensilla. Area not ringed of dentes nearly five times the length of mucro. Claw elongate, with two paired basal teeth; tenent hair acuminate. Reduced formula:  $R_0R_1R_2000/00/0101+2/s$ ,  $-aBq_1q_2$ ,  $M_1m_2R^*el_1l_2$  (\* 1/3 to 2/3 of M; sometimes  $M_1$  smooth and  $L_2$  ciliated, and usually asymmetrically).

**Description. Habitus** (Figs 3, 4A). Body length up to 3.1 mm (holotype: 2.3 mm). Colour: blue pigment laterally on body from Th II to Abd IV, but extended to dorsal part in Th II, coxae I–III, first third of femur III, laterally on head and vertex and Ant I–III. Abd IV paler. Eyes and a spot on central vertex strongly pigmented.

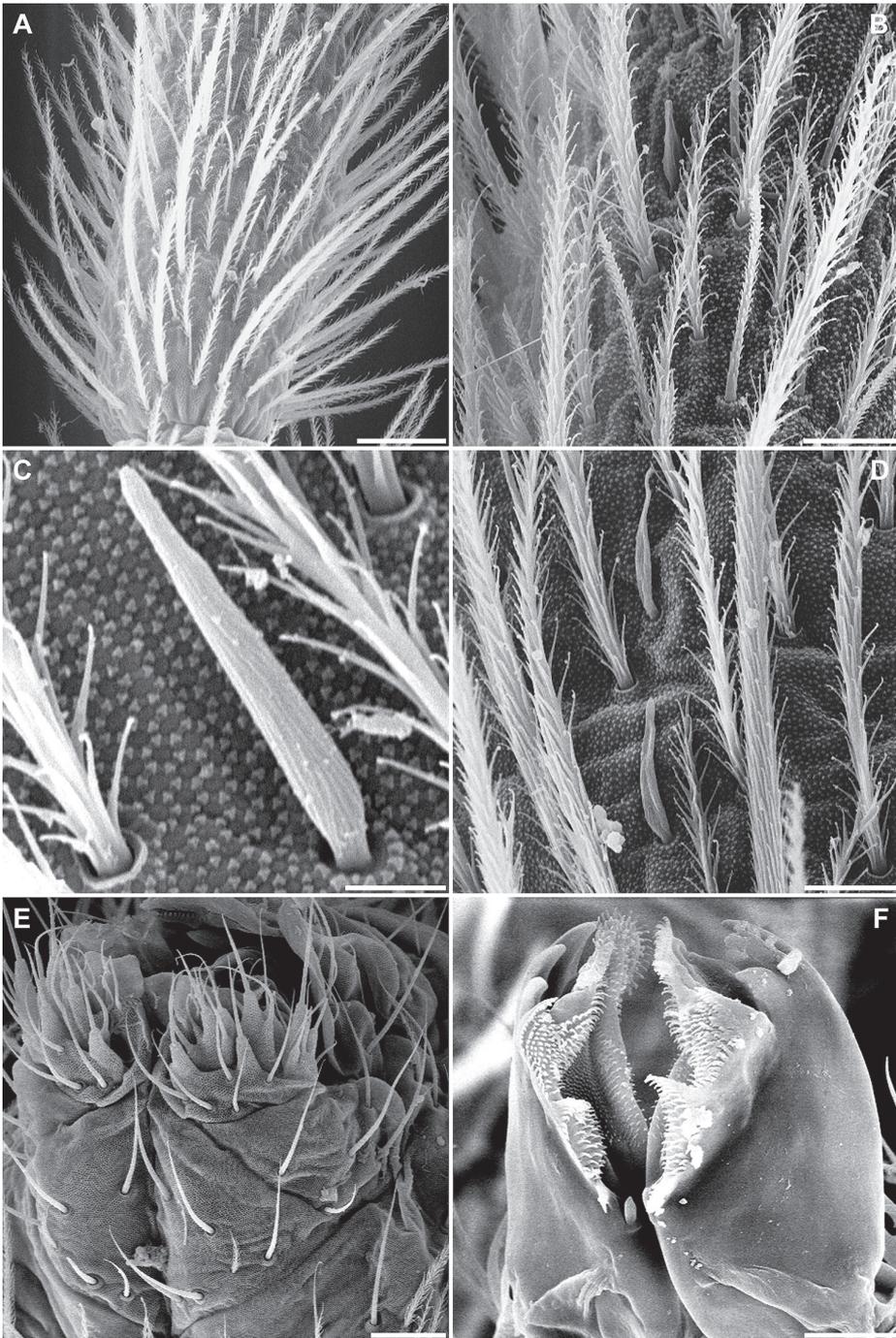
**Head.** With five eyes (ABDEF or ABCDF; C and F smaller, almost imperceptible in some specimens). Intraocular chaetae p, r, and s present. Only  $A_0$ ,  $A_2$ ,  $A_3$ ,  $An_1$ ,  $An_2$ ,  $An_{3a}$ , and  $An_3$  as Mc (Fig. 7C). Ratio antenna/cephalic diagonal 1.64–2.16. Antennal



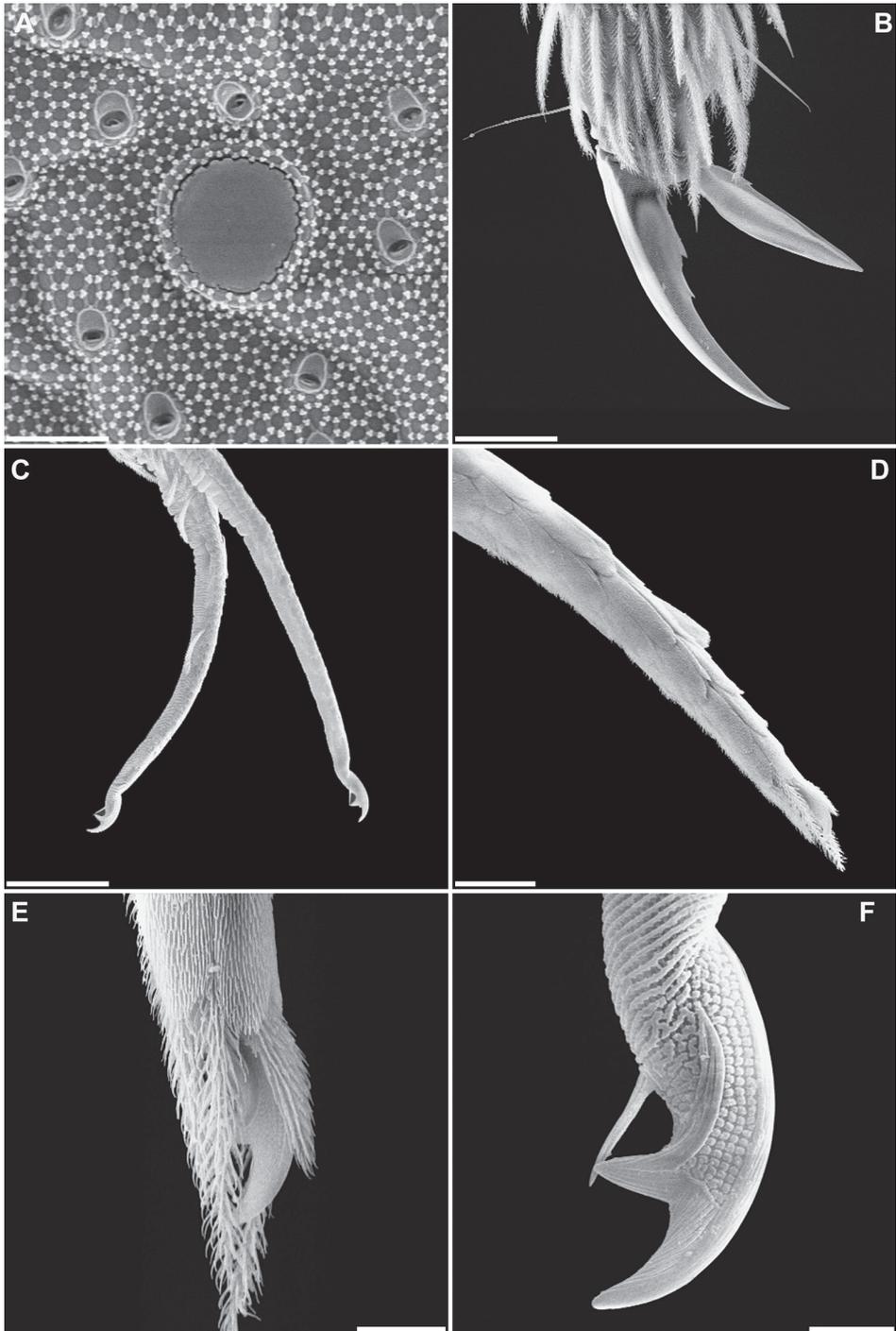
**Figure 4.** *Pseudosinella altamirensis* sp. nov. **A** habitus **B** distal part of tibia-tarsus III and claw complex **C** trochanteral organ. Scale bars: 0.5 mm (**A**); 0.02 mm (**B, C**).

segments I/II/III/IV ratios 1/2–2.7/2.3–2.7/3.5–4.1. Ant IV proximal area in Fig. 5A; apical vesicle absent (Fig. 7A); in this segment there are up to four special leaf-shaped sensilla on the distal third, two of them aligned, and at least five other different types of sensilla (some described by Beruete et al. 2002): smooth and cylindrical, some with short fringes, clearly different from the normal chaetae (Fig. 5B); smooth, shorter and narrowed in its distal third (Fig. 5C); and leaf-shaped, similar to the sensorial chaetae ‘s’ of sensory organ of Ant III (Fig. 5D). Ant III sense organ with a peculiar configuration: two paddle-shaped sensilla (individually encased in a pit and more or less one above the other), another two similar ones but in a dorso-internal position, and two small, rounded, spiny guard sensilla on both sides of the first one (Fig. 7B). Apical region of the Ant II–III with pseudopore in internal-ventral position, far from chaetae line. Antennae without scales. Prelabral chaetae ciliated; labral row a, m, and p all smooth (distal row (a) on papillae). Formula of the labial base  $M_1m_2Rel_1l_2$ ;  $M_1$  sometimes smooth, asymmetrical in some specimens; R ciliated, 1/3 to 1/2 length of the neighbouring smooth  $Mc_m$ ;  $l_1$  occasionally ciliated; the remaining chaetae smooth, but with minute fringes or ciliation seen only in SEM (Fig. 5E). Bifurcate maxillary palp with three smooth sublobal chaetae. Labial papilla (l.p.) E with finger-shaped process just reaching the base of apical appendage. Maxilla in Fig. 5F.

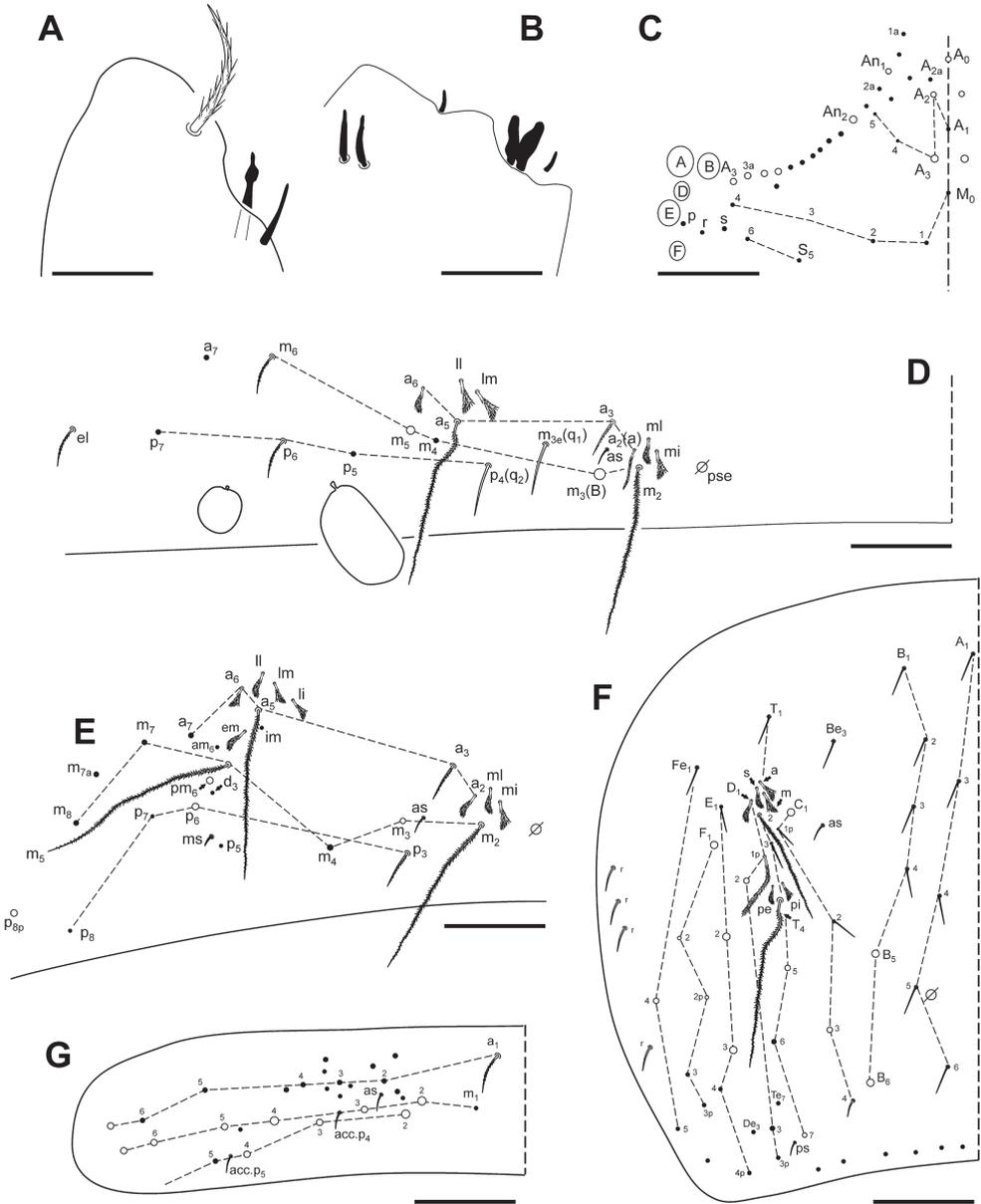
**Body.** Th II without  $Mc$ ; pseudopore of this tergite in Fig. 6A. Th III without  $Mc$ . Abd II: chaetae a,  $q_1$  and  $q_2$  as ciliated mic, chaeta B as broad ciliated  $Mc$  (Fig. 7D). Abd III chaetotaxy shown in Fig. 7E. Accessory chaeta ‘s’ in the anterior trichobothrial



**Figure 5.** *Pseudosinella altamirensis* sp. nov. **A** proximal half of Ant IV **B** detail of Ant IV showing normal chaetae and different types of sensilla: leaf shaped, smooth, with small cilia **C** detail at high magnification of the small sensilla narrowed at tip found on Ant II–IV **D** two leaf-shaped sensilla on Ant IV **E** labium and labral palps **F** maxillae. Scale bars: 0.02 mm (**A**, **E**); 0.007 mm (**B**); 0.002 mm (**C**); 0.006 mm (**D**); 0.009 mm (**F**).



**Figure 6.** *Pseudosinella altamirensis* sp. nov. **A** Th II pseudopore **B** claw and empodium appendage of leg III **C** distal par of dens and mucro **D** tip of dens and mucro, not visible by the covering scales of terminal dens **E** mucro partially covered by scales and chaetae **F** mucro and mucronal spine. Scale bars: 0.004 mm (**A, F**); 0.02 mm (**B, D**); 0.04 mm (**C**); 0.007 mm (**E**).



**Figure 7.** *Pseudosinella altamirensis* sp. nov. **A** antennae, tip of Ant IV **B** antennae, Ant III sensory organ **C** head, dorsal chaetotaxy; Abdomen dorsal chaetotaxy: **D** abd II **E** abd III **F** abd IV **G** abd V. White dots, Mc (size of the socket proportional to reality); black dots, mic. Scale bars: 0.01 mm (**A**); 0.02 mm (**B**); 0.05 mm (**C-E**); 0.1 mm (**F, G**).

complex of Abd IV present. Medial chaeta B<sub>5</sub> below the level of the trichobothrium T<sub>4</sub>. Pseudopore between B<sub>5</sub> and B<sub>6</sub>. Legs scales only on coxae. Trochanteral organ with ca 30 chaetae (Fig. 4C). Remaining chaetae clearly visible on all legs, acuminate and largest on leg III. Differentiated supraempodial inner chaeta on hind tibiotarsus well differentiated

and acuminate. Dorsal tibiotarsal tenent hairs acuminate, 0.3 times the length of inner margin of claw. Claw with only three internal teeth: dental plate occupying 35% of the basal internal edge, with the basal paired teeth of different sizes (posterior one larger and slightly more distal than anterior); unpaired tooth well developed, approximately 40% from base; lateral tooth, anterior, less frequently posterior, present in some specimens on leg I and in basal positions; dorsal tooth basal, observed only in one specimen at SEM. *Empodium* appendage acuminate, basally swollen, externally smooth, with a minute tooth in some specimens (Figs 4B, 6B). Retinaculum with 4 + 4 teeth and one ciliated chaeta. Ventral tube without scales; lateral flap with a maximum of eight smooth and six ciliated chaetae. Manubrium and dens with scales only ventrally (anteriorly); two internal and 7–12 external chaetae related to two distal pseudopores of manubrial plate; area not ringed of dentes nearly five times the length of mucro; mucro with distal tooth longer than the anteapical; basal spine reaching the tip of distal tooth (Fig. 6C–F). Chaetotaxy from head to Abd V illustrated in Fig. 7C–G.

**Biology.** This species is always found over organic matter accumulation. In Cudón cave, it has been found over the residue of rotten and wet wood; in the other caves it was found over old, mouldy rat and bat faeces and generally in insect cadavers with visible fungi. Although this species reaches to the dark zone of the caves near very wet areas, it has been found in deep zones on walls, roofs, and soils where the environmental humidity is near the saturation point (Fig. 2). The species appears to be restricted to the karst systems associated with the Saja River and within the municipal districts of Miengo, Santillana del Mar, Reocín, and Cabuérniga (Luque and Labrada 2016) (Fig. 1).

**Etymology.** The name is toponymical and refers to the type locality, the Altamira Cave, one of the most important Palaeolithic art sites in Europe.

## Discussion

According to the dorsal macrochaetotaxy (R000/00/0101+2), the presence of chaeta 's' in the anterior trichobothrial complex of the Abd IV, the Abd II chaetotaxy (-aBq<sub>1</sub>q<sub>2</sub>), and the formula of the labial base (M<sub>1</sub>m<sub>2</sub>Rel<sub>1</sub>l<sub>2</sub>; M<sub>1</sub> or m<sub>1</sub>; L<sub>1</sub>o l<sub>1</sub>), this species is similar to *Pseudosinella goughi* Gisin & Gama, 1972, *P. suboculata* Bonet, 1931, and *P. superoculata* (with more constant labial base formula: M<sub>1</sub>m<sub>2</sub>Rel<sub>1</sub>l<sub>2</sub> except in the case of *P. goughi* with M<sub>1</sub> or m<sub>1</sub>). Nevertheless, these three species have six eyes (A, B, C, D, E, and F). *Pseudosinella suboculata* can have five eyes, but its dorsal tibiotarsal tenent hair is clavate and its claw is clearly different, with longer paired teeth, impaired tooth distal (more than 60% from base of inner claw), and the empodium appendage not basally swollen. *Pseudosinella superoculata* has the paired teeth of the inner claw at the same level, claw approximately 30% longer than in the new species, manubrial plate with three chaetae (two in one specimen) internal to pseudopore, and sensorial chaetae 's' of sensory organ of Ant III rod-like (after Gisin and Gama 1969 and observed also in some specimens from the Cantabria and Navarra caves). *Pseudosinella goughi* exceptionally has up to seven eyes and only two internal teeth on claw. In addition, the

**Table 1.** Equivalence table of Gisin (1965, 1967a, 1967b) notation formulae for chaetotaxy to the modern notation of Soto-Adames 2010 (AMS) as presented in the figures.

| Dorsal Mc formula                |  |  |  |  |  |  |  |  |  |  |  |  | Additional sensilla |  |  |  | Abd II formula |  |  |  |
|----------------------------------|--|--|--|--|--|--|--|--|--|--|--|--|---------------------|--|--|--|----------------|--|--|--|
| Head                             |  |  |  |  |  |  |  |  |  |  |  |  | Abd                 |  |  |  |                |  |  |  |
| Th                               |  |  |  |  |  |  |  |  |  |  |  |  | Abd IV +            |  |  |  |                |  |  |  |
| Th II / Th III /                 |  |  |  |  |  |  |  |  |  |  |  |  | Abd IV /            |  |  |  |                |  |  |  |
| 0-2 / 0-2                        |  |  |  |  |  |  |  |  |  |  |  |  | 0-3                 |  |  |  |                |  |  |  |
| mic-Mc number                    |  |  |  |  |  |  |  |  |  |  |  |  | mic-Mc number       |  |  |  |                |  |  |  |
| m or p series                    |  |  |  |  |  |  |  |  |  |  |  |  | row B               |  |  |  |                |  |  |  |
| m or p series                    |  |  |  |  |  |  |  |  |  |  |  |  | C <sub>1</sub>      |  |  |  |                |  |  |  |
| Pa <sub>5</sub>                  |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M <sub>5</sub> or S <sub>4</sub> |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M                                |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>2</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>1</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>0</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| Pa <sub>5</sub>                  |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M <sub>5</sub> or S <sub>4</sub> |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M                                |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>2</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>1</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>0</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| Pa <sub>5</sub>                  |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M <sub>5</sub> or S <sub>4</sub> |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M                                |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>2</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>1</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>0</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| Pa <sub>5</sub>                  |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M <sub>5</sub> or S <sub>4</sub> |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M                                |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>2</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>1</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>0</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| Pa <sub>5</sub>                  |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M <sub>5</sub> or S <sub>4</sub> |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M                                |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>2</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>1</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>0</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| Pa <sub>5</sub>                  |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M <sub>5</sub> or S <sub>4</sub> |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M                                |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>2</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>1</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>0</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| Pa <sub>5</sub>                  |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M <sub>5</sub> or S <sub>4</sub> |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M                                |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>2</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>1</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>0</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| Pa <sub>5</sub>                  |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M <sub>5</sub> or S <sub>4</sub> |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| M                                |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
| A <sub>2</sub>                   |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
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| M                                |  |  |  |  |  |  |  |  |  |  |  |  |                     |  |  |  |                |  |  |  |
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four special leaf-shaped sensilla present on Ant IV in the new species separate it from its most similar species. With the same dorsal macrochaetotaxy, but without chaeta 's' on Abd II, there are six species: *P. alpina* Gisin, 1950 (one eye); *P. astronomica* Gisin & Gama, 1970 (one eye); *P. christiani* Stomp, 1986 (without eyes); *P. mucronata* Gouze & Deharveng, 1987 (five or six); *P. thibaudi* Stomp, 1977 (two eyes); and *P. vandeli relicta* Gisin, 1964 (no eyes). The differences between these nine species and the new species are shown in Table 1.

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# New species and records of *Cloeodes* Traver, 1938 (Ephemeroptera, Baetidae) from Costa Rica

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## Abstract

The nymph of *Cloeodes danta* **sp. nov.** is described from male and female nymphs collected from highland streams in the Caribbean Slope of the Costa Rica Central Volcanic Mountain Range. Adults are unknown. In addition, *C. excogitatus* and *C. redactus* are recorded for the first time in the country. *Cloeodes danta* **sp. nov.** can be differentiated from all described species by the predominantly brownish coloration on females and a similar coloration on males but with segments VII–IX light yellow and light brown, with no conspicuous marks or patterns; abundant scale-bases throughout most parts of the body; hindwings pads absent; the presence of three spines in the corners of the posterior margin of sternum III, and the posterior margin of tergum III with 28–30 spines on each side of the middle line (spine with a base width up to 0.5× spine length).

## Keywords

diversity, freshwater, mayflies, Neotropics, taxonomy

## Introduction

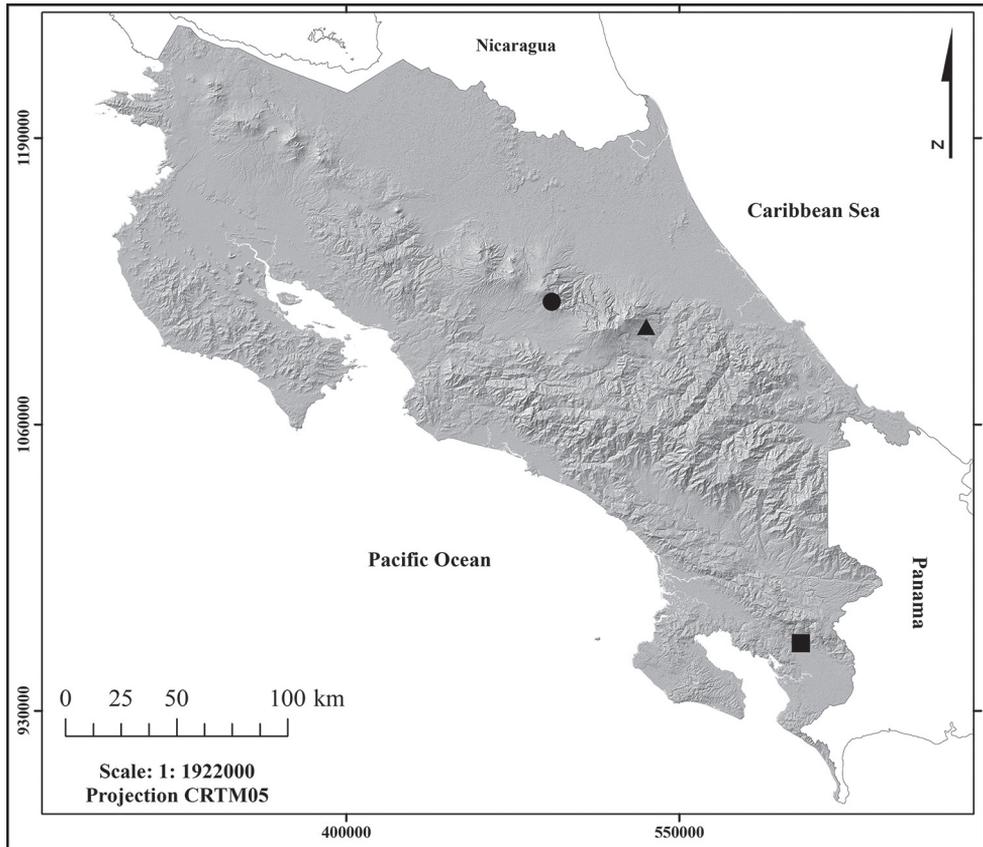
The genus *Cloeodes* (Ephemeroptera, Baetidae) was erected by Traver (1938) for a group of species described from Puerto Rico with hind wings absent. Later, the genus was reviewed by Waltz and McCafferty (1987) and established for other species distributed across the Neotropics, Southern Nearctic, Afrotropics, and Oriental region. More recently, through phylogenetic analysis the genus has been depicted as exclusive for the New World within a complex including *Bungona* spp., *Crassolus* spp. and *Potamocleoen* spp. (Salles et al. 2016). Currently, the number of *Cloeodes* species has doubled in the last ten years with 26 species described for the Neotropics (Salles et al. 2016; Kluge 2017).

Despite the increase in the number of papers related to *Cloeodes* and the report of 142 mayfly species in Central America and the Caribbean (Cornejo and Flowers 2015; Salles et al. 2016), there are only two *Cloeodes* species formally reported from the Central American region: *C. excogitatus* (Waltz & McCafferty, 1987) and *C. redactus* (Waltz & McCafferty, 1987), registered from Guatemala and Honduras, respectively (McCafferty and Lugo-Ortiz 1996; McCafferty et al. 2004). In Costa Rica, the presence of the genus has been recorded for lowland and midland streams with scarce human intervention and good water quality (McCafferty et al. 1992; Flowers and De la Rosa 2010), but no species have been formally reported until now.

During an ongoing study of the richness and taxonomy of the family Baetidae in Costa Rica, nymphs of a new *Cloeodes* species and nymphs of *C. excogitatus* and *C. redactus* were collected in low order streams. This work provides a complete description of this new species and diagnostic characters for distinguishing *C. excogitatus* and *C. redactus*, in order to improve the taxonomic knowledge of the genus for future natural history or ecological studies of mayflies, which have crucial knowledge gaps in the tropics (Balian et al. 2008; Ramírez and Gutiérrez-Fonseca 2014).

## Material and methods

Nymphs of these species were collected using a hand net to scrape large stone substrates from different streams in Costa Rica (Fig. 1). Line drawings for the new species description were made from original pictures taken with an AmScope 1803 digital camera adapted to a Premiere (MRP–161) microscope and stereomicroscope Premiere SMZ-05. The type material examined is preserved in 80% ethanol and Euparal permanent slides, and it has been deposited in Museo de Nacional de Costa Rica, San José Province; Laboratorio de Entomología (LEUNA), Escuela de Ciencias Biológicas, Universidad Nacional, Heredia; Museo de Zoología, Universidad de Costa Rica; and Purdue University Entomological Research Collection (PERC), West Lafayette, Indiana, USA.



**Figure 1.** Geographic distribution in Costa Rica of *Cloeodes danta* sp. nov. (black circle), *Cloeodes excogitatus* (black triangle) and *Cloeodes redactus* (black square).

## Results

### *Cloeodes danta* Vásquez-Bolaños, Sibaja-Araya & Guevara-Mora, sp. nov.

<http://zoobank.org/F2F0FC62-E8EE-4E79-93F6-48F711DAC45C>

Figures 2–6

**Material examined.** *Holotype*: mature ♂ nymph slide-mounted in Euparal, Costa Rica, Heredia Province, Central Volcanic Mountain Range, Cerro Chompipe zone, Refugio de Vida Silvestre Cerro Dantas, Río Las Vueltas, 10°5'38.24"N, 84°3'42.57"W, 2000 m above sea level, VI/09/2017, Sibaja-Araya F. and Acuña F. (colls), deposited in Museo de Nacional de Costa Rica, San José Province. *Paratypes*: 5 mature nymphs same data as holotype, preserved in 95% alcohol (mouthparts, legs, gills, terga and paraprocts in micro-vial) deposited at Laboratorio de Entomología (LEUNA), Escuela de Ciencias Biológicas, Universidad Nacional, Heredia (1♂, 1♀); Museo de Zoología, Universidad de Costa Rica (1♀) and PERC, West Lafayette, Indiana, USA (1♂, 1♀).

**Additional material.** Nine nymphs, Quebrada Grande, Refugio de Vida Silvestre Cerro Dantas, 10°5'38.24"N, 84°3'42.57"W, about 1 km from the Río Las Vuelatas at 2054 m asl, where type material was collected, Heredia Province, Costa Rica V/13/2018, F. Sibaja, D. Romero, M. Guevara, D. Segura, O. Vázquez (colls), deposited at Laboratorio de Entomología (LEUNA) of the Escuela de Ciencias Biológicas, Universidad Nacional.

**Diagnosis. Mature nymph.** 1) Brownish body coloration, without conspicuous marks or patterns (Fig. 2), 2) abundant scale-bases throughout most parts of the body (Figs 5b, 6h, 6i, 6k), 3) Absence of hind wing pads, 4) Tibia with two parallel lines of fine long hairs (Fig. 5b), 5) posterior margin of tergum III with 28–30 spines on each side of the middle line (Fig. 6h), 6) sterna with 26–28 variable size spines on each side of the middle line and three thick, spine-like teeth in each corner of the posterior margin of sternum III (Fig. 6i, 6j), 7) paraproct with about 13–15 spines (Fig. 7k).

**Description.** (based on last instar male and female nymphs; adults unknown).

**Size** (Mature nymphs): Body length: 5.3–6 mm males, 5.5–6.2 mm females; antennae 1.5–1.7 mm; cerci 2.4–2.7 mm; terminal filament 2.2–2.5 mm.

**Body coloration:** Brownish in general (Fig. 2A, 2B), the head light brownish, with clearer area from central ocelli to the border of clypeus and between antennal and labrum bases; ocelli black, with two tiny white symmetrical dots on each side and clear brownish coloration, darker toward ocellus; eyes black, turbinated portion of compound eyes brownish. Fore wing pads brownish, foreleg brown with slightly lighter areas. Abdomen with even brownish coloration on females and males with predominantly brownish color but with segments VII–IX light yellow and light brown, both with no patterns of marks or spots, and upper corners of abdominal segments darkened; terga I–VIII with visible black posterior sigilla in the middle of every segment, terga VII–IX lighter with upper corners darkened; sterna pale yellowish-brown.

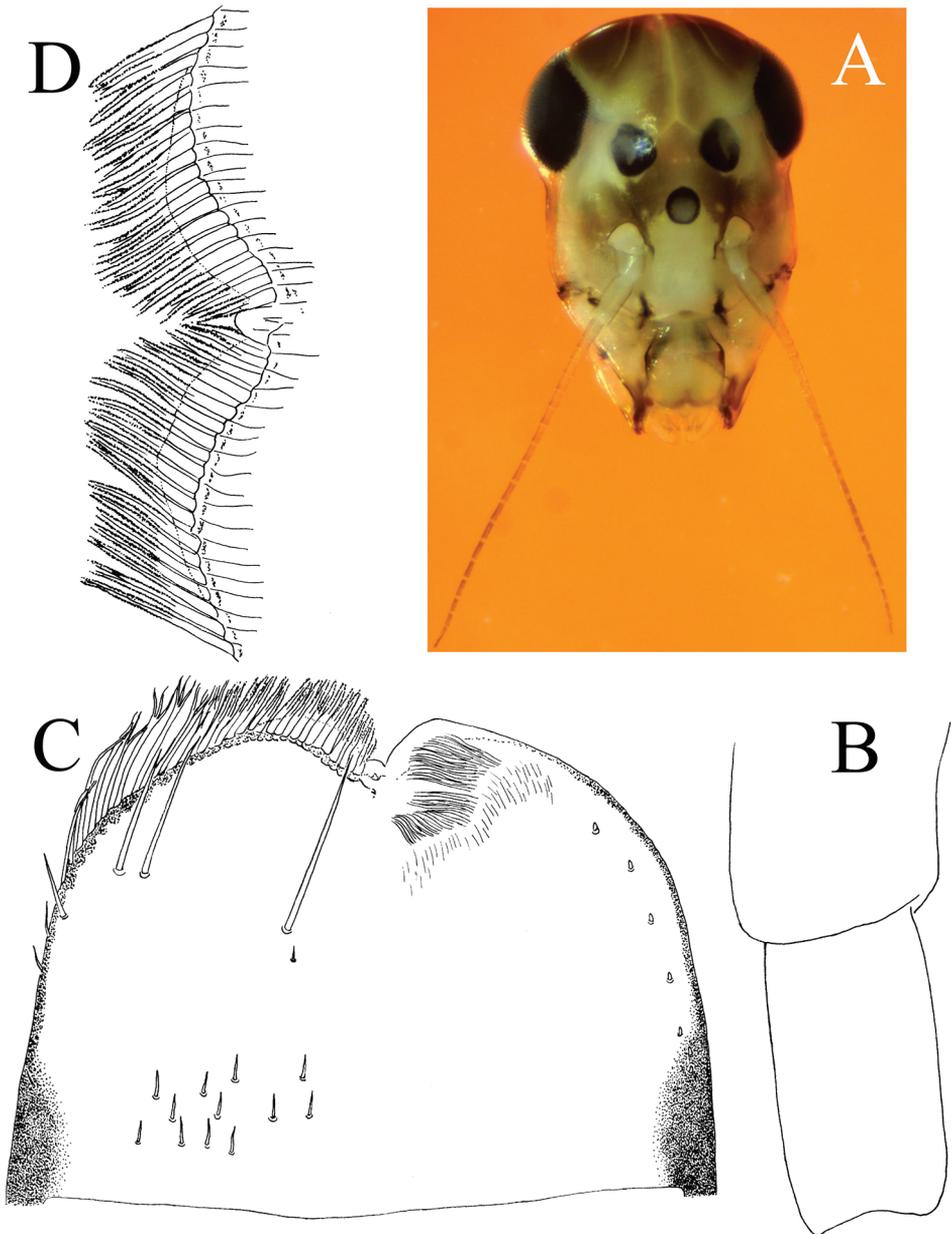
**Head** (Fig. 3A): Capsule longer than wide. Antennae subequal to 1.3× length of head, with scape subequal to 1.3× times length of pedicel (Fig. 3B). Intra-antennal extension of frons prolongs to ocelli.

Labrum (Fig. 3C). Subrectangular, broader than long, anterolateral margins rounded; dorsally with anterior margin with about 20 small, double frayed setae. Lateral margin with eight apically frayed setae; arc of anterodorsal setae with four simple setae; intermediate seta tiny; and several small scattered simple setae near posterior margin. Ventrally with small curved fine setae near anterior margin, and seven small simple setae near lateral margin. Anterior margin slightly asymmetric, with the left side of the cleft not extended the same length as the right side (Fig 3D).

Left mandible (Fig. 4A). Incisors with seven denticles, middle one reduced and others similar in size; prosthema robust, apically with three lobes and four elongated projections. Row of 5 or 6 minute spine-like setae between prosthema and molar region, only visible at high magnification (40×). Ventral surface of molar region with tuft of spines next to thumb as part of molar structure (Fig. 4B).

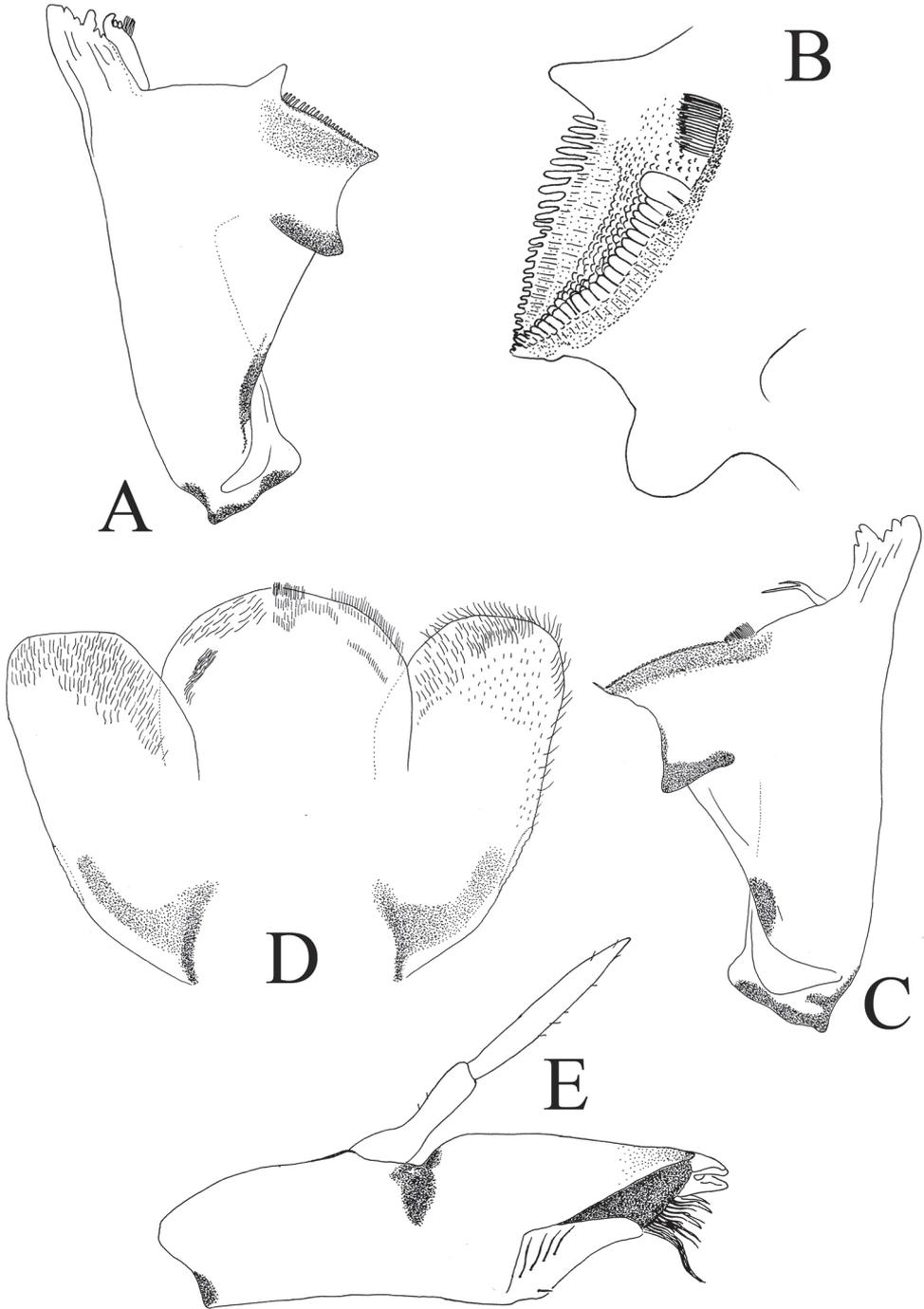


**Figure 2.** *Cloeodes danta* sp. nov. Body coloration **A** male **B** female.

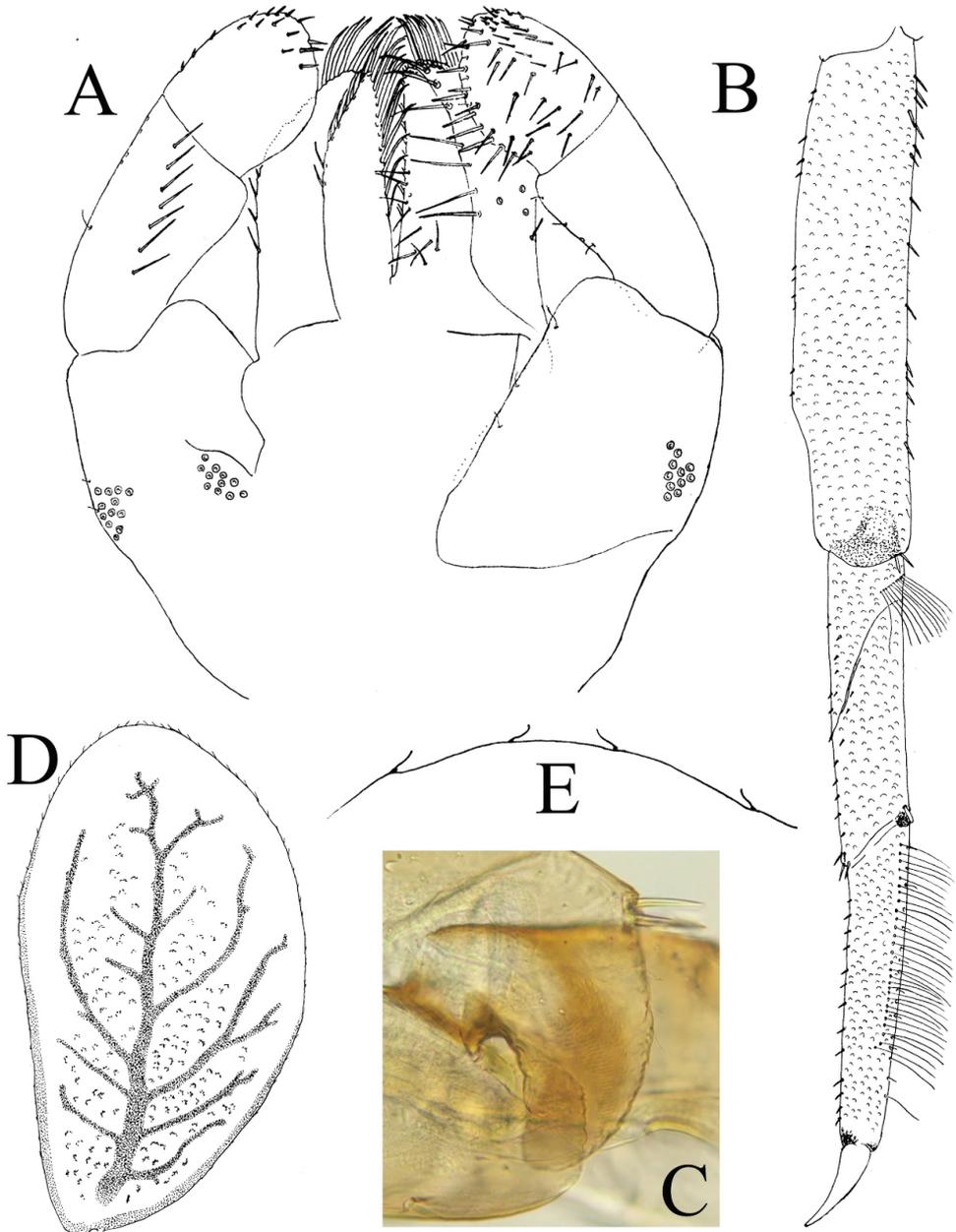


**Figure 3.** *Cloeodes danta* sp. nov. **A** head color pattern and intra-antennal extension detail **B** scape and pedicel **C** labrum (left d. v., right v. v.) **D** detail of labrum asymmetry on anterior margin.

Right mandible (Fig. 4C). Incisors with seven denticles, middle one reduced and others similar in size; prostheca with broad base, bifid, inner projection longer, and both parts frayed; 3–4 tiny, simple setae between prostheca and molar region only visible at high magnification (40×); tuft of spines next to molar region.



**Figure 4.** *Cloeodes danta* sp. nov. **A** left mandible **B** detail of molar region, left mandible **C** right mandible **D** hypopharynx (left d. v., right v. v.) **E** maxilla.



**Figure 5.** *Cloeodes danta* sp. nov. **A** labium (left d. v., right v. v.) **B** foreleg **C** forefemur apex detail **D** gill III **E** gill III apex detail.

Hypopharynx (Fig. 4D). Lingua rounded with no apical lobes, slightly longer and broader than superlinguae, both apically covered with short fine hairs on dorsal and ventral surface.

Maxillae (Fig. 4E). Palpi slightly shorter or as long as galea-lacinia, two segmented; segment I slender in mid part; segment II 1.4× length of segment I; both segments with several simple short setae. Crown of galea-lacinia without thick distal denticles, with numerous setae on the inner-dorsal and inner ventral rows, and longer and slender towards the biting edge; medial region of galea-lacinia with one short seta and 5 or 6 long, simple setae.

Labium (Fig. 5A). Glossa and paraglossa similar in length, basally broad and apically narrow; with the base of the glossa reaching more than half of the paraglossa; glossae dorsally with 7–8 setae next to the inner margin and some scattered setae, ventrally with 12 or 13 setae on the inner margin and 9 or 10 on the outer margin, increasing in length apically in both cases. Paraglossae curve inwards, apex subtriangular, dorsally with 7 or 8 setae on the inner margin and 17 or 18 setae on outer margin. Palpi with segment I broad and 0.8× length of segment II and III combined, numerous micropores and simple, tiny setae on both dorsal and ventral surfaces; segment II with row of 6 or 7 setae on the dorsal surface; segment III suboval, dorsally with several short simple setae on apex and 20–25 simple setae of different size on the ventral surface, and the inner margin subequal to the outer margin.

**Thorax:** Hindwing pads absent; foreleg with abundant scale-bases and scattered micropores (Fig. 5B). Femur length about 4× maximum width; dorsal edge with 10 or 11 short, simple setae, ventrally bare, apex rounded with no evident projections, and two concave and apically rounded setae. Tibia with two lines of fine hairs arranged parallel to each other along the tibia, subtending bristle elongated and rounded (Fig. 5B, C). Tarsi dorsal edge bare, ventrally with 10 or 11 minute spines, increasing in size distally; tarsal claw length 0.5× length of tarsi. Mid and hind legs are similar to the foreleg.

**Abdomen:** Gills (Fig. 6A–G). Present on segments I–VII, colorless, oval, margins with curved fine setae (Fig. 6D, 6E); light-brown tracheae extending from main trunk, branching to margins. Gill I smaller than segment II; gill IV length about 1.3× length of segment III; gills on segment VII not extending beyond apex of segment X (Fig. 2A, B).

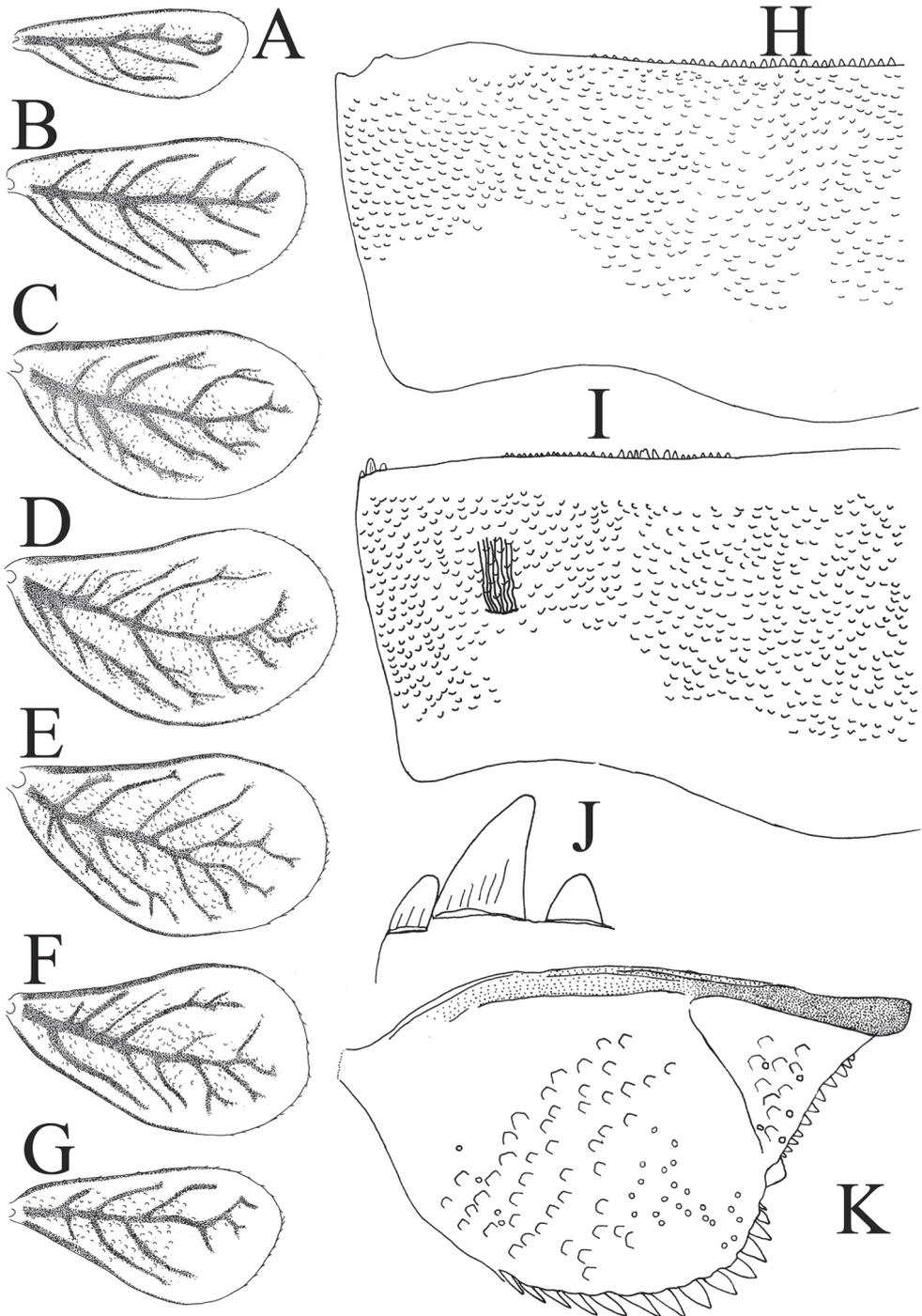
Terga. Tergum I with no spines on posterior margin; tergum III with 28–30 spines on posterior margin of each side of the middle line, spine bases almost same width as height (Fig. 6J).

Sterna (Fig. 6I). Posterior margin of sternum III with group of 26–28 variable size spines on each side of middle line, spine bases width about one-third of height; group of fine hairs arranged in slightly curved line on each side of sterna and three thick spine-like teeth on each corner of posterior margin of sternum III (Fig. 6H).

Paraprocts (Fig. 6K). Lateral margin with 13–15 spines, different in size and arranged in irregular line, with some overlapping; dorsal surface with numerous micropores and scale-bases; posterolateral extension with about 11 or 12 marginal spines, and several scale-bases and micropores.

**Adults.** Unknown.

**Etymology.** The name of this species honors the Danta (*Tapirus bairdii*) (Mammalia: Tapiridae), a common species in the Cerro Chompipe cloud forest zone, whose three-toed back feet resemble the sternal spine-like teeth described as a diagnostic character of *C. danta* sp. nov.



**Figure 6.** *Cloeodes danta* sp. nov. **A** gill I **B** gill II **C** gill III **D** gill IV **E** gill V **F** gill VI **G** gill VII **H** abdominal tergum III **I** abdominal sternum III **J** detail of sternum spine-like teeth **K** paraproct.

**Distribution.** Costa Rican, Caribbean slope basin, first order streams, above 2000 m asl.

**Biology.** Habitat preferences in *C. danta* sp. nov. were observed in relation to elevation. Individuals were found at 2054 m asl in cold waters of two cloud forest streams (Fig. 7); other non-Andean species have been reported between 159–1800 m asl (Nieto and Richard 2008; Gutiérrez and Reinoso-Flórez 2010; Massariol and Salles 2011; Massariol et al. 2013; De Paul et al. 2013; Gutiérrez and Dias 2015). Also, the new species was collected in a pristine forest region, which may be similar to other *Cloeodes* species in Brazil that seem to prefer remnant forest areas (Salles et al. 2015). In addition, *C. danta* sp. nov. is common in riffles, on igneous boulders that are covered with periphyton; this is typical for this genus, part of the grazer functional feeding group (Baptista et al. 2006).

### *Cloeodes excogitatus* (Waltz & McCafferty, 1987)

*Cloeodes excogitatus* Waltz & McCafferty, 1987: 200; McCafferty and Lugo-Ortiz 1996: 23; Wiersema and Baumgardner 2000: 61; McCafferty et al. 2004: 207.

**Material examined.** *Paratype*, *Cloeodes excogitatus*, R.W. Koss and R. Baumann, 1 ♂ / Collected 12/V/1968, Arizona, Oak Creek Canyon, slide-mounted in Euparal (Abs. Alc.) by R.B. Waltz VI/1983, det. by Waltz and MacCafferty, 1984. (Paratype),



**Figure 7.** Habitat of *Cloeodes danta* sp. nov. at Río Las Vueltas.

PERC (0,012,327). *Cloeodes excogitatus*, DE Baumgardner, 1 male/ 1 female / Collected 21/V/2004, Arizona, Geenlee CO. San Francisco R. at FS Road, 212, ca 1 mi. N. Clifton. 33°04'30"N, 109°18'04"W, Elev. 3700 ft, (DB04-21), det. M. Meyer 2005. 10 mature nymphs, Río Torito, La Fuente, Santa Teresita, Turrialba, Cartago, Costa Rica, 9°59'13.04"N, 83°40'44.95"W, 1063 m asl, II/28/2017. Romero D. and Sibaja-Araya F. (colls). Material in 95% alcohol, deposited at Laboratorio de Entomología (LEUNA), Escuela de Ciencias Biológicas, Universidad Nacional, Heredia, Costa Rica.

**Distribution.** Guatemala, Mexico, USA (Waltz and McCafferty 1987; McCafferty and Lugo-Ortiz 1996; Wiersema and Baumgardner 2000; McCafferty et al. 2004), and Costa Rica.

### *Cloeodes redactus* (Waltz & McCafferty, 1987)

*Cloeodes redactus* Waltz & McCafferty, 1987: 204; McCafferty and Lugo-Ortiz 1996: 23; Nieto and Emmerich 2011: 58; Massariol et al. 2013: 11; Forero-Céspedes et al. 2016: 462; Kluge 2017: 104.

**Material examined.** Five mature nymphs, Río Claro tributary, Río Claro, Golfito, Puntarenas, Costa Rica. 8°41'13.05"N, 83°02'48.78"W, 79 m asl, XII/25/2018. Coll. Sibaja-Araya F. (coll.). Material in 95% alcohol deposited at Laboratorio de Entomología, Escuela de Ciencias Biológicas (LEUNA), Universidad Nacional, Heredia, Costa Rica.

**Distribution.** Colombia, Honduras, Peru (Waltz and McCafferty 1987; McCafferty and Lugo-Ortiz 1996; Massariol et al. 2013; Forero-Céspedes et al. 2016; Kluge 2017), and Costa Rica.

## Discussion

*Cloeodes danta* sp. nov. shares morphological affinities with the following species: *C. caraibensis* Hofmann et al. 1999, *C. excogitatus*, *C. redactus*, and *C. maculipes* Traver, 1938, including, absence of hind wing pads, segment III of labial palp rounded, maxillary palp shorter than galea-lacinia, and the general shape of other structures like labrum, labium and the apex of the femur that were recognized by Hofmann et al. (1999) and Nieto and Richard (2008). Based on the material and literature reviewed, we consider that Central American and Caribbean species can be separated in two groups according to the depth of the central cleft on the right mandible incisives: in *C. excogitatus* and *C. redactus* the cleft breaks down below the level of mandible first inner incisor apex (Waltz and McCafferty 1987: fig. 27; Kluge 2017: fig. 66), while in *C. danta* sp. nov., *C. caraibensis* and *C. maculipes* the cleft breaks down at the level of the first inner incisor apex (Waltz and McCafferty 1987: figs 3, 4; Hofmann et al. 1999: fig. 37; Fig. 4C).

In regard to *C. caraibensis* from Lesser Antilles, these species mentioned above have setae on segment III of the labial palp as long as the setae on the glossa and paraglossa

(Waltz and McCafferty 1987: fig. 6; Hofmann et al. 1999: fig. 41), while in *C. danta* these setae are shorter (Fig. 5A). Also, labrum intermediate setae are well developed in *C. maculipes* (Waltz and McCafferty 1987: fig. 2), while in *C. danta* sp. nov. they are minute (Fig. 3C); in regard to *C. caraibensis* this character is absent, and this species also shares some diagnostic characters with *C. danta* sp. nov. like scale-bases present on most of the body, shape of III segment of labial palp and spines on the corner of the posterior margins of the sterna (Hofmann et al. 1999: figs 36, 41, 50); however, *C. danta* sp. nov. can be differentiated by no spots or color pattern on the abdomen, right mandible prosthema with two well-developed branches, glossa apically not lobulated, distal portion of gills rounded, minute spines on the terga and sterna margins, and the posterior margin of the paraproct with no bifurcated spines (Figs 2A, 2B, 4C, 4D, 6A–6G, 6K).

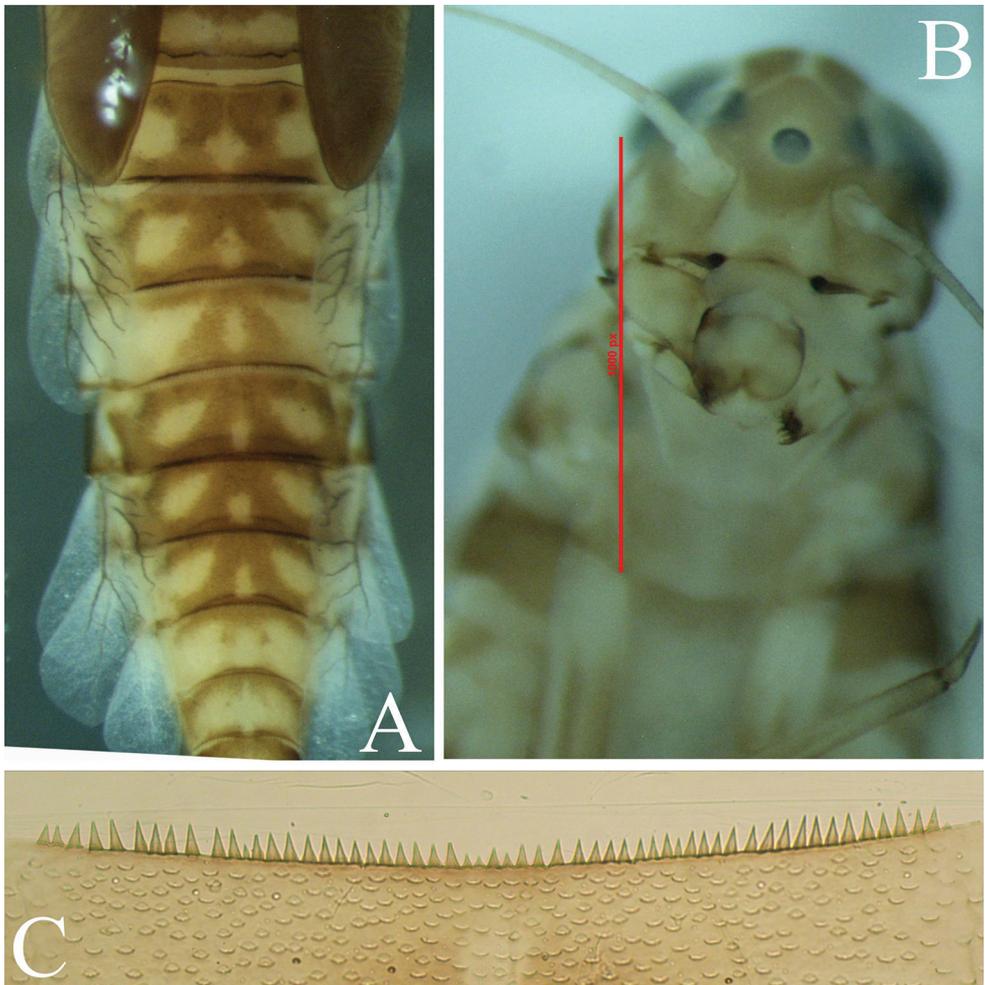
Furthermore, *C. danta* sp. nov. shares similar features with *C. excogitatus*, such as the number of spines in the terga III, the shape segment III of labial and the abundance of setae on it (20–25), the number of spines in the paraproct, and body size (Waltz and McCafferty 1987, but *C. danta* sp. nov. can be identified by the different abdominal color pattern, abundant scale-bases throughout most parts of the body, the maxillar palp is equal in length to the galea-lacinia and the absence of a narrow intra-antennal extension. Also, the new species resembles *C. redactus* in the length of the maxillary palp being about as long as the galea-lacinia, the number of spines in the paraproct and the lack of any projections on the apex of the femur (Waltz and MacCafferty 1987; Kluge 2017); however it could be distinguished by the shape and number of spines in terga III, the absence of the colorless spots in some terga, a larger body size, the presence of an intermediate setae on the labrum, and the presence of thick spine-like teeth in the inferior corner of sterna III.

In order to improve the identification of *Cloeodes* species in the Central American region, we provide a key to distinguish *C. danta* sp. nov., *C. excogitatus* and *C. redactus*. This will be a useful tool for future aquatic research in the region, which has been increasing over the last 20 years due to development of water quality monitoring using aquatic insects (Alonso-Eguía et al. 2014; Carrie et al. 2017; Castillo 2018; Dávila-Recinos et al. 2019; Pérez 2019).

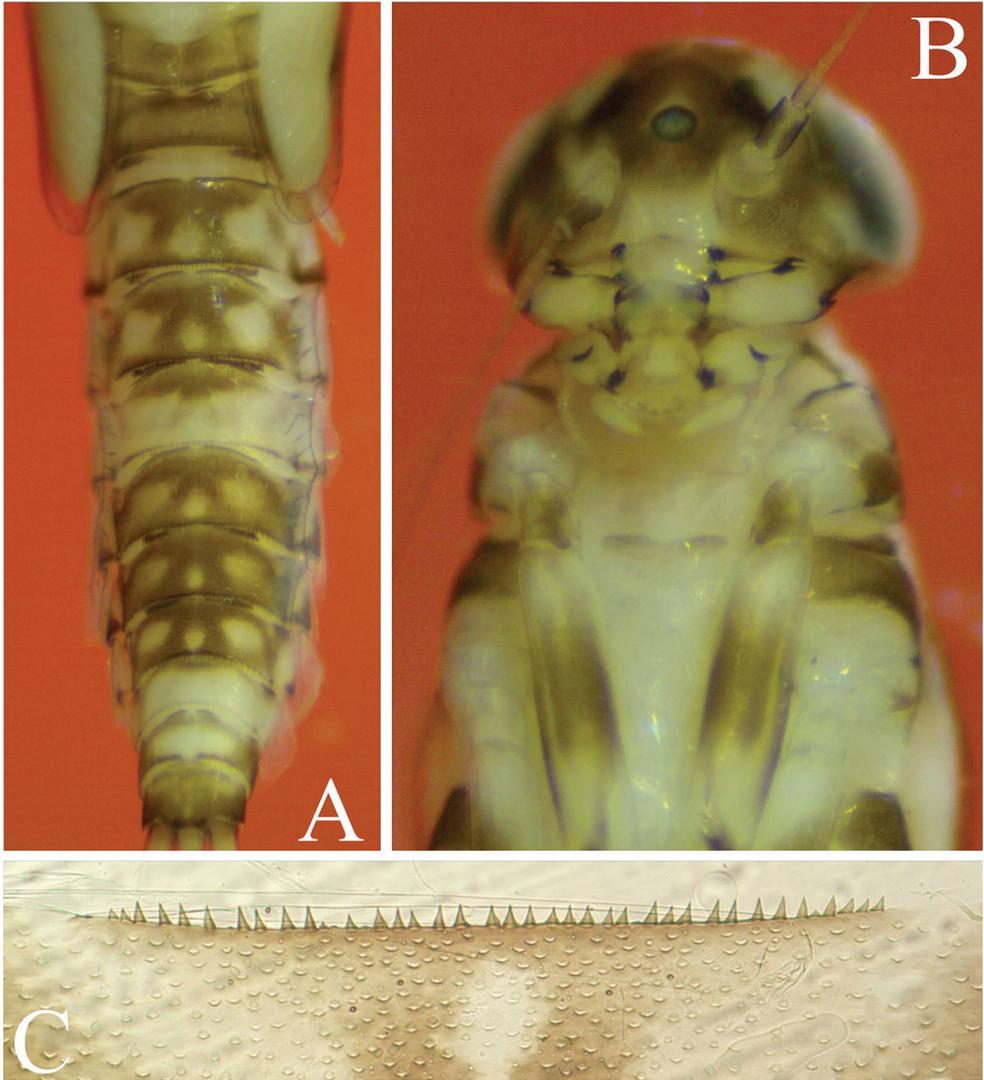
### Key to mature nymphs of *Cloeodes* species in Central America

- 1 Abdomen with brownish uniform color pattern, without spots or distinctive marks; body covered with scale-bases; intermediate setae minute; cleft on right mandible incisive breaks down at level of first inner incisor apex and thick spines like teeth present in sternal III corners (Figs 2A, 2B, 4C, 6I, 6J); highlands (2054 m asl) ..... ***C. danta* sp. nov**
- Abdomen with marks or spotted color pattern (Figs 8A, 9A); body not covered with scale-bases cleft on right mandible incisives breaks down below level of mandible first inner incisor apex; intermediate setae absent; no spines on sternal corners of sterna III (Waltz and McCafferty 1987; Kluge 2017); mid or lowlands ..... **2**

- 2 Abdominal coloration on terga I–III and V–VII with 3 pale spots (the middle spot being smaller); intra-antennal extension narrow, labrum arc of anterodorsal setae with 5 simple setae; segment III of labial palp ventrally with 20–25 setae; maxillary palp shorter than galea-lacinia; 30–35 spines on tergum III (Fig. 8B, C; Waltz and McCafferty 1987: figs 25, 36, 40); midlands (1063 m asl) ..... *C. excogitatus*
- Abdominal coloration with terga I–III and V–VII with dark brown transverse stripes on posterior margins; intra-antennal extension not narrowed; labrum arc of anterodorsal setae with 3 simple setae; segment III of the labial palp with 30–35 setae; maxillary palp about same length as galea-lacinia; 15–20 spines on tergum III (Fig. 9B, C; Kluge, 2017: figs 6, 12, 14, 58, 59); lowlands (79 m asl) ..... *C. redactus*



**Figure 8.** *Cloeodes excogitatus*: **A** abdomen coloration **B** intra-antennal extension (scale:1000 pixels : 2 mm) **C** spines on tergum III.



**Figure 9.** *Cloeodes redactus*: **A** abdomen coloration **B** intra-anteral extension **C** spines on tergum III.

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# A third species of the rarely collected Oriental hoverfly genus *Furcantenna* Cheng, 2008 (Diptera, Syrphidae, Microdontinae)

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## Abstract

*Furcantenna malayana* **sp. nov.** is described from Peninsular Malaysia, based on a single female collected in 1962. The other two known species of this genus are also known from single specimens, from South-eastern China and Nepal. A key to the species is given, and the taxonomy and distribution of the genus are discussed.

## Keywords

Identification key, Malaysia, morphology, new species, taxonomy

## Introduction

Few species of Syrphidae are known in which the basal antennal flagellomere (the apical segment of the antenna, which carries the arista) is furcate. In the subfamily Eristalinae a bifurcate basal antennal flagellomere is only found in males of the genus *Cacoceria* Hull, 1936. All other instances of this remarkable character among Syrphi-

dae are restricted to the subfamily Microdontinae. In this subfamily, the character is known in the New World genera *Carreramyia* Doesburg, 1966, *Masarygus* Brèthes, 1909, *Schizoceratomyia* Carrera, Lopes & Lane, 1947 and an unnamed genus; in the Australian genus *Cervicorniphora* Hull, 1945; and in the Oriental genus *Furcantenna* Cheng, 2008 (Reemer and Ståhls 2013a).

The genus *Furcantenna* was described based on a single male specimen of *F. yangi* Cheng, 2008, collected in 1982 in the Guangxi Province in the Oriental part of China (Cheng and Thompson 2008). The second species, *F. nepalensis* Reemer, 2013, was described based on a single male specimen collected in 1967 in Nepal (Reemer and Ståhls 2013a). Ongoing taxonomic research in various entomological collections by the author revealed a third specimen of the genus, belonging to a third species, collected in 1962 in Peninsular Malaysia. This species is described here, and a key to distinguish it from the other two *Furcantenna* species is given.

## Material and methods

The studied specimen is deposited in the collection of the California Academy of Sciences (CAS) in San Francisco, USA. Photos of the specimen were made through a Zeiss Stereo Discovery v12 microscope, and processed (focus stacking) by Axiovision (version SE64 4.9) software. The map was made in Adobe Illustrator, based on locality information in Cheng and Thompson (2008), Reemer and Ståhls (2013a) and the present article (the symbols for the localities were placed by approximation, as available locality information is imprecise). Measurements of the studied specimen were taken using an ocular micrometer in a Wild M3B stereo microscope. Body length was measured from the anterior part of head (excluding antenna) to the apex of the abdomen. Morphological terminology follows Cumming and Wood (2017). For the type specimen, label data are given in quotation marks (“...”) and line breaks on the label are indicated with a slash (/).

## Results

### Generic diagnosis

The genus *Furcantenna* is characterized by the combination of the following characters: wing vein  $R_{4+5}$  without posterior appendix; wing vein  $M_1$  straight, perpendicular to wing vein  $R_{4+5}$ ; abdomen broadly oval; antenna inserted below dorsal eye margin; basal antennal flagellomere much longer than scape, longer than distance between antennal socket and anterior oral margin; scutellum apicomediaally sulcate; metasternum developed.

The pilosity of the katepisternum is variable: bare in *F. yangi* (Cheng and Thompson 2008), pilose in the other two species. The pilosity of the metasternum is also variable: bare in *F. malayana* sp. nov., pilose in the other two species.

Key to the species of *Furciantenna*

- 1 Face and vertex black. Wing in apical half dark, at least anteriorly. Metasternum pilose. Katepimeron pilose or bare ..... **2**  
 – Face medially and vertex partly yellow (Figs 1–4). Wing in apical half whitish (Fig. 7). Metasternum bare. Katepimeron pilose ..... ***F. malayana* Reemer, sp. nov.**  
 2 Body colour brownish without violet shine. Katepimeron pilose. Scutellum slightly sulcate ..... ***F. nepalensis* Reemer**  
 – Body colour blackish with violet shine. Katepimeron bare. Scutellum deeply sulcate ..... ***F. yangi* Cheng**

***Furciantenna malayana* sp. nov.**

<http://zoobank.org/DED6DB6F-ADDA-4027-A0CB-295956C9CC47>

Figures 1–8

**Material. Holotype:** MALAYSIA. • 1 ♀, holotype of *Furciantenna malayana* sp. nov.; SE of Ipoh; alt. 50 m; 10 Oct. 1962; E.S. Ross & D.Q. Cavagnaro leg.(CAS).

Label 1: “MALAYA: 3 mi. / SE. Ipoh / 50m VII-10-62”; label 2: “Collectors: / E.S. Ross / D.Q. Cavagnaro”.

**Diagnosis.** *Furciantenna malayana* is the only known species of the genus with a partly yellow face and vertex, and a bare metasternum. The whitish apical half of the wing is also characteristic.

**Description. Adult female.** Body length: 9 mm (Fig. 1).

**Head.** Face occupying slightly more than 1/2 of head width in frontal view; yellow medially, dark brown laterally; silvery white pilose. Oral cavity with lateral margins not produced. Frons medially yellow, bare; laterally dark brown, golden yellow pilose. Vertex swollen; yellow, except brown around ocellar triangle; yellow pilose. Occiput dark brown; yellow pilose. Eye bare, except for a few scattered, very short pile, only visible under high magnification (Fig. 4). Antennal socket about 1.5× as high as wide. Antenna brown; ratio of scape:basal flagellomere approx. 1:2.1; basal flagellomere swollen at apical 1/4, appearing club-shaped, with apex approx. twice as wide as base. Arista yellowish, about 3/4 as long as basal flagellomere (Fig. 3).

**Thorax.** Postpronotum yellowish brown; yellow pilose. Mesoscutum brown, quite pale along margins and more blackish in middle; golden yellow pilose in anterolateral corners and along posterior margin, leaving a black pilose area in the shape of an upside-down letter T in between (Fig. 5). Postalar callus yellowish brown; yellow pilose. Scutellum without calcars, with shallow apicomedian sulcus; pale brown; black pilose (Fig. 6). Pleuron brown. Anterior and posterior part of anepisternum divided by a weak sulcus; almost entirely yellow pilose, except bare on narrow strip along dividing sulcus and on small ventral part. Anepimeron on anterior part with mixed yellow and black pile, other parts bare. Katatergum and anatergum long and short microtrichose, respectively. Katepisternum dorsally whitish pilose, ventrally bare. Katepimeron white pilose. Metasternum bare (except for dark microtrichia). Mediotergite dark brown;



**Figures 1–8.** *Furcantenna malayana* sp. nov., female, holotype **1** habitus dorsal **2** habitus lateral **3** head frontal **4** head lateral **5** thorax dorsal **6** scutellum dorsal **7** wing **8** abdomen dorsal.



**Figure 9.** Known localities of *Furcantenna* species.

shining, except narrowly microtrichose anteriorly and on rudimentary subscutellum. Calypter grey. Halter pale yellow.

**Wing.** Brown in basal half, whitish in apical half (Fig. 7). Microtrichose, except bare on posterobasal 1/2 of cell br.

**Legs.** Pale brown, except hind femur and tibia darker brown; black pilose, except ventral surface of tarsi yellow pilose. Hind tibia strongly swollen, widest in the middle, with dorsal pile much longer than on other parts of the legs (Fig. 2). Coxae and trochanters brown; black pilose.

**Abdomen.** Pale brown (Fig. 8). Tergites short pilose: tergite 1 yellow pilose; tergite 2 black pilose except yellow pilose along anterior margin; tergite 3 black pilose; tergites 4 and 5 yellow pilose. All sternites yellow pilose.

**Etymology.** The specific epithet is an adjective which refers to Malaysia, the country where the species was collected.

**Distribution.** Only known from Peninsular Malaysia (Fig. 9).

## Discussion

The description of *Furcantenna malayana* is based on the first known female of the genus. Even though the basal antennal flagellomere is not furcate, as it is in the males of the other two described species of *Furcantenna*, the specimen is considered to belong to

this genus. The combination of the following characters supports this placement: wing vein  $R_{4+5}$  without posterior appendix; wing vein  $M_1$  straight, perpendicular to wing vein  $R_{4+5}$ ; abdomen broadly oval; basal antennal flagellomere longer than distance between antennal socket and anterior oral margin; scutellum apicomediaally sulcate; katepisternum pilose. Also, in most Neotropical counterparts of *Furcantenna* (species of *Carreramyia*, *Masarygus* and *Schizoceratomyia*) the furcate antenna is found only in males, with the exception of *Schizoceratomyia malleri* (Curran, 1947) and *Masarygus carrerai* Papavero, 1962 (the female of the Australian genus *Cervicorniphora* is unknown).

*Furcantenna* was placed in a clade with the Neotropical genera *Carreramyia*, *Masarygus*, and *Schizoceratomyia* in a phylogenetic analysis based on morphological characters (Reemer and Ståhls 2013b). If these genera are indeed closely related, this would be a case of a trans-Pacific distribution pattern as defined by Cranston (2005). Similar examples among Microdontinae are found in the subgenus *Chymophila* Macquart, 1834 of *Microdon* Meigen, 1803, and in the genus *Paramicrodon* de Meijere, 1913 (Reemer 2012).

Apparently the genus *Furcantenna* is quite widespread in the Oriental region, even though the species are very rarely collected. Whether their elusiveness is a result of very restricted ranges, occurrence in very low densities, or a lifestyle that makes them difficult to notice, remains a matter of speculation.

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# A taxonomic revision of the whitefish of lakes Brienz and Thun, Switzerland, with descriptions of four new species (Teleostei, Coregonidae)

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## Abstract

The alpha taxonomy of the endemic whitefish of lakes Brienz and Thun, Switzerland, is revised. We evaluate the status of seven known species: *Coregonus steinmanni* **sp. nov.**, *Coregonus profundus* **sp. nov.** and *Coregonus acrinus* **sp. nov.** are endemic to Lake Thun; *Coregonus brienzi* **sp. nov.** is endemic to Lake Brienz; and *C. alpinus*, *C. albellus*, and *C. fatioi* from lakes Brienz and Thun are redescribed. One of these species, *C. alpinus*, is revised, since the lectotype for this species is incongruent with the species description given by Kottelat (1997) and Kottelat and Freyhof (2007). The name *C. alpinus* is thus retained for the lectotype designated by Kottelat (1997) and a new description of this taxon provided. For the species otherwise described by Kottelat (1997) and Kottelat and Freyhof (2007) as *C. alpinus* the new name *C. profundus* is designated. *Coregonus acrinus* is genetically partially of allochthonous origin, closely related to the radiation of Lake Constance, and we therefore compare it to all recognized species of Lake Constance, *C. wartmanni*, *C. macrophthalmus*, *C. arenicolus*, and *C. gutturosus*.

## Keywords

adaptive radiation, *Coregonus*, ecological speciation, taxonomy, whitefish

## Introduction

The European whitefish (*Coregonus spp.*) provide prime examples of postglacial adaptive radiations, with several lakes in the boreal, subarctic and prealpine climate zones harbouring multiple, often closely related and endemic species. Up to six species can occur in single lakes of the pre-alpine region (Hudson et al. 2016; Dönz et al. 2018), and perhaps even more in the largest lakes of north-east Europe (Bernatchez 2004; Hudson et al. 2007; Kottelat and Freyhof 2007). Many of these radiations diversified after the most recent retreat of the ice shields 10'000 to 15'000 years ago (Bernatchez 2004; Østbye et al. 2005; Hudson et al. 2011). Diversification was by a combination of geographically sympatric and allopatric speciation in boreal and subarctic lakes (Østbye et al. 2005; Præbel et al. 2013) and mainly by geographically sympatric speciation from an ancestral hybrid population in pre-alpine lakes (Hudson et al. 2011). Multiple axes of divergence appear to structure whitefish radiations in Europe that repeatedly and independently evolved ecologically similar sets of species (“ecomorphs” sensu William 1972) which exhibit parallel patterns of divergence in traits related to foraging (i.e., gill raker number, benthic vs. limnetic feeding ecology), physiology (i.e., growth rate, depth partitioning during feeding and breeding) and reproductive ecology (i.e., spawning season and spawning habitat varying along lake depth and along the benthic-pelagic axis) (Fatio 1890; Steinmann 1950; Østbye et al. 2005; Vonlanthen et al. 2009, 2012; Harrod et al. 2010; Lundsgaard-Hansen et al. 2013; Hudson et al. 2016; Dönz et al. 2018; Öhlund et al. 2020). The two common combinations of traits among species in European whitefish radiations are large, fast growing, sparsely gill-rakered, benthivorous fish spawning in shallow water versus small sized, slow growing, densely rakered, zooplanktivorous fish spawning in deep water, but other combinations of some of these traits can also be found in some species (Steinmann 1950; Vonlanthen et al. 2012; Hudson et al. 2016). The number of gill rakers on the first gill arch have shown to be heritable (Rogers and Bernatchez 2007; Roesch et al. 2013). Variation in this trait relates to variation in the relative efficiency of feeding on zooplankton and benthic prey items (Lundsgaard-Hansen et al. 2013; Roesch et al. 2013). Interspecific differences in body shape (Lundsgaard-Hansen et al. 2013) as well as in growth rates resulting in different body size at a given age have both been shown to be heritable too (Rogers and Bernatchez 2007; Lundsgaard-Hansen et al. 2013). A large number of molecular genetic tests of reproductive isolation among sympatric whitefish species in various Swiss lakes have confirmed that sympatric forms are generally genetically clearly differentiated species (Douglas and Brunner 2002; Douglas et al. 2003; Hudson et al. 2011; Vonlanthen et al. 2012; Hudson et al. 2016; Dönz et al. 2018; Feulner and Seehausen 2018; Jacobs et al. 2018; De-Kayne et al. unpublished).

Here, we revise the whitefish species of lakes Brienz and Thun, Switzerland. Whitefish can be found in the large pre-alpine lakes of France, Germany, Austria, and Switzerland, which historically harboured approximately 50 different species native to approximately 30 lakes in three major river drainages: the Rhine, the Danube, and the Rhone (Svärdson 1957; Kottelat and Freyhof 2007; Winkler et al. 2011; Vonlanthen

et al. 2012). Part of this species diversity has been lost during increased lake eutrophication in the last century (Vonlanthen et al. 2012). Phylogeographic studies have shown that the European *C. lavaretus* species complex, which diverged from the North American *C. clupeaformis* species complex at least 500,000 years ago, comprises of two divergent mitochondrial lineages (Bernatchez and Dodson 1991, 1994; Douglas et al. 2003; Østbye et al. 2005; Kottelat and Freyhof 2007; Hudson et al. 2011; Winkler et al. 2011). The two lineages overlap in their geographical distribution, whereby the “northern lineage” (mitochondrial N clade) is predominantly found in Scandinavia and the Baltic Sea region while the “central European lineage” (C clade) has a higher frequency of occurrence in the pre-alpine and North Sea region, hence more westerly (Hudson et al. 2011). The entire pre-alpine whitefish radiation is a monophyletic radiation as revealed by genomic AFLP-markers and whole-genome resequencing data when compared to the closest relatives from northern Germany and Scandinavia (Hudson et al. 2011; De-Kayne et al. unpublished). The occurrence of both central and north mitochondrial haplotype lineages within the pre-alpine radiation, today (Hudson et al. 2011) as well as already 5000 years ago (Alonso et al. 2017), and the frequent occurrence of both lineages within species of the radiation suggest that the entire pre-alpine radiation is of hybrid origin (Hudson et al. 2011). The ancient carriers of the two divergent mitochondrial lineages probably correspond to two glacial refugial lineages that came into secondary contact and hybridized before the hybrid population spread across much of western Europe and diversified into the modern species flocks. As the Alpine ice shields retreated, this hybrid population would have colonized the pre-alpine lakes and radiated within each of the larger lakes into several endemic species (Hudson et al. 2011). As a result, both haplotypes are shared among many of the approx. 25 contemporary endemic species that are native to 17 Swiss lakes (Steinmann 1950; Kottelat and Freyhof 2007; Hudson et al. 2011; Vonlanthen et al. 2012). Only one century ago Swiss lakes harboured approximately 35 endemic species of whitefish, but one third of this original diversity has been lost in the middle of the 20<sup>th</sup> century due to a combination of speciation reversal through hybridization and demographic declines, both driven by loss of habitat for foraging and spawning and possibly of selective regimes, associated with anthropogenic eutrophication of lakes (Vonlanthen et al. 2012; Hudson et al. 2013; Alexander et al. 2017).

In this paper we compile and review morphological, genetic and ecological data for seven species of whitefish from the connected lakes Thun and Brienz, three of which are found in both lakes. Three of the species were previously described as *C. alpinus* Fatio, 1885, *C. albellus* Fatio, 1890, and *C. fatioi* Kottelat, 1997. We describe four new species that are endemic to one of the two lakes. Three of them are endemic to Lake Thun, *C. steinmanni*, *C. profundus* and *C. acrinasus*. One is endemic to Lake Brienz, *C. brienzii*.

One of the previously described species, *C. alpinus* was designated a lectotype by Kottelat (1997) for which the species description (biology and morphology) in Kottelat (1997) and Kottelat and Freyhof (2007) is incongruent and not that of this species. We show this by tracing back Fatio’s description of *C. alpinus* in his compendium on

Swiss fauna (1890) and comparing it to the lectotype of *C. alpinus* and to contemporary samples of this species.

One of the newly described species, *C. acrinasus*, shows ancestry contributions from whitefish of Lake Constance, besides its Lake Thun ancestry (Hudson et al. 2011, 2016; Dönz et al. 2018). We therefore do not only compare it to the five other species from Lake Thun but also to the four described species from Lake Constance, namely *C. wartmanni* Bloch, 1784, *C. macrophthalmus* Nüsslin, 1882, *C. arenicolus* Kottelat, 1997, and the extinct *C. gutturosus* Gmelin, 1818.

We studied the type material designated by Kottelat (1997) in his systematic revision of the nomenclature of European freshwater fishes for the three described species from lakes Thun and Brienz, *C. alpinus*, *C. albellus*, and *C. fatioi* and the four described species from Lake Constance, *C. wartmanni*, *C. macrophthalmus*, *C. arenicolus*, and the extinct *C. gutturosus*. Altogether, we compared 240 of our own contemporary samples from lakes Thun and Brienz to these type series.

## Materials and methods

### Study lakes and fish collection

Type material of all currently valid species (based on Kottelat's (1997) systematic revision of the nomenclature of Swiss whitefish) was inspected in the collections of the Natural History Museum of Geneva and Bern (**MHNG** and **NMBE**, respectively), Switzerland and in the Steinmann collection of Eawag, Switzerland, that has recently been transferred together with the Seehausen-Eawag collection to the Natural History Museum of Bern (**NMBE**), Switzerland. All contemporary specimens are part of the Seehausen-Eawag collection. In some cases, more than one fish is stored in the same jar and thus we provide next to the NMBE number in brackets the individual labels of each fish with Eawag followed by the individual number.

The different whitefish species in this study derive from different lakes, namely Lake Thun (46°40'N, 7°46'E, surface area 48 km<sup>2</sup>, max depth 217m), Lake Brienz (46°43'N, 7°57'E, surface area 30 km<sup>2</sup>, max depth 261 m), Lake Biel (47°5'N, 7°10'E, surface area 39.3 km<sup>2</sup>, max depth 74 m) and Lake Constance (47°38'N, 9°22'E, surface area and max depth of Upper Lake Constance 473 km<sup>2</sup> and 251 m and of lower Lake Constance 63 km<sup>2</sup> and 46 m depth). Lakes Thun and Brienz are among the deepest and most oligotrophic lakes of the northern pre-alpine region. Lake Constance was historically also among the most deep and oligotrophic lakes of the northern pre-alpine region but is today a mesotrophic lake (Vonlanthen and Périat 2013; Vonlanthen et al. 2015; Alexander et al. 2016). Lakes Thun and Brienz are connected through a short stretch of river (the Bödéli Aare) forming a super-lake system, and used to be part of a much larger postglacial lake, Lake Wendel, before high bed rock load from the river Lütschine separated the basin into the current two lake basins several thousand years ago (Steinmann 1950; Ammann et al. 1991; Hantke and Sc-

heidegger 2007). The species flock of the two lakes, except for *C. acrinus*, forms a monophyletic group based on independent multilocus microsatellite, large AFLP and whole genome datasets (Douglas et al. 2003; Hudson et al. 2011; Hudson et al. 2016; De-Kayne et al. unpublished). Furthermore, within the super-lake system, the populations of each species from the two sister lakes, Thun and Brienz, are more closely related to each other than the different species from the same lake (i.e., species monophyly), suggesting that the origin of the radiation predates separation of Lake Wendel into lakes Brienz and Thun (Hudson et al. 2011; Hudson et al. 2016; Dönz et al. 2018).

Contemporary samples of whole specimens from lakes Thun and Brienz were collected in the course of many projects of the Seehausen research group (Eawag and the University of Bern). Contemporary material (whole specimens and tissue samples) used here was collected in the years 2005, 2011, 2013, 2014 and 2015 in lakes Thun and Brienz, and in 2016 in Lake Biel. Some of the fish were obtained from commercial fisheries catches. Additionally, in lakes Thun and Brienz fishing was done with monofilament bottom- and pelagic gill nets of various mesh size ranging from 5 to 60 mm, and across many depth ranges in the limnetic and benthic habitats of the lakes (details on net fishing protocols can be found in Alexander et al. (2015)). The fish come from three different sampling methods: targeted fishing on known spawning grounds of the different species at the respective spawning season and water depth (Hudson et al. 2011; Hudson 2011; Vonlanthen et al. 2012), targeted fishing each at one spawning site in lakes Thun and Brienz along a depth gradient four times during the whole spawning season of all species (this study), and habitat-stratified fishing of the whole lake during the summer months (Vonlanthen and Périat 2013; Vonlanthen et al. 2015; Dönz et al. 2018). Additionally, individuals of some species were retrieved from local fisherwomen or fishermen. The sampling locations of all contemporary specimens are plotted on a map in the Suppl. material 1: Figure S10.

## Sample processing

Sampling details for the fish collected in the years 2005, 2011, 2013, and 2014 can be found in the corresponding publications (Bittner 2009; Hudson 2011; Vonlanthen et al. 2012; Dönz et al. 2018). For the fish collected in the year 2015 and 2016 the procedure was as follows: upon capture, fish were anaesthetised and subsequently euthanised with appropriate concentrations of MS222 solutions. Muscle tissue and scales below the dorsal fin, as well as a part of the pectoral fin on the right side of the body, were taken for genetic and isotopic analysis and to determine the age of each fish. The left side of each fish was photographed in two ways: once in water in a custom-made photo cuvette and once on a flat surface with the fins spread. Fish were then fixed in 4% formalin solution for at least 1 month and afterwards transferred through a series of ethanol of increasing concentration (30%, 50%) to the final concentration of 70% for storage. Permits for collecting fish in the lakes were issued by the canton of Bern.

In the field the fish were identified to species level as good as possible. Sex, fresh mass (to the nearest 0.1g), ripeness (4 = not ripe; 5 = partially ripe, i.e., slow flow of egg and sperm when stripped; 6 = ripe, i.e. eggs and sperm flow easily when stripped) and the presence of tubercles on the scales (modified from Kekäläinen et al. 2015: 0 = not present; 1 = small to medium-sized tubercles; 2 = large tubercles) were noted in some but not all of the field campaigns. Fish which were not ripe, and thus where the sex could not be determined externally, were examined internally by opening the abdominal cavity and inspected for the presence of testis or ovaries.

The age of the specimens that were used in this study was determined in the lab by counting the annual growth rings of four scales under a confocal microscope following Lehtonen and Nylund (1995). If the ages differed between the four scales and three out of four scales did not correspond to the same age, further scales were measured to acquire the same age in 75% of the scales.

## Morphological and meristic characters

Morphological measurements and counts on the old type material (N = 31) and on contemporary specimens (N = 340) were taken of 25 body, 19 head, and 4 gill characters with a digital calliper to the nearest 0.1 mm. Twelve meristic characters were counted. The measurements and counts were taken on the left body side of the fish, unless a specific character was missing or deformed, in which case that character was measured or counted on the right side of the fish. The mean of two measurements were taken for each character, whereby the difference between two measurements had to be less than 5%. If agreement was less good, the distance was measured again two times. The average inaccuracy between two measurements taken over all morphological characters was 1.4%. Not all measurements could be taken for several specimens since characters were damaged or absent, and we thus sometimes report incomplete character lists for certain specimens. This results in varying sample sizes for each character. All characters for which we had missing values were not retained in the multivariate ratio analyses (see below). The number of characters used for each analysis is explicitly mentioned in the results section. Most of the morphological and meristic characters follow Hubbs and Lagler (1964). However, we also included some additional characters and refined the measurement of some characters found in Hubbs and Lagler (1964). A brief description of each character can be found in Table 1 for the morphological characters and in Table 2 for the meristic characters. Furthermore, illustrations in Suppl. material 1: Figures S1, S2 depict the measurements of the morphological characters. For all morphological characters the mean and for all meristic characters the mode are reported together with the standard deviation and the range for each species, lake population, and sex. Some times if the sample sizes were too small, no mode could be calculated and thus, we report “na”. For the four newly described species, the holotype is included in the range. Both sexes are included for the full range of each character of each species from both lakes Thun and Brienz.

**Table 1.** Morphological characters, their acronyms and a brief description of each character.

| Morphological characters                                    | Acronym | Description  |
|---|---------|--|
| <b>Body</b>   |         |  |
| Pelvic fin base   | PelvFB  | Length between insertions of fin   |
| Pelvic fin "spine" length                                   | PelvFS  | Length from upper insertion point of fin to tip of spine; the spine is actually an elongated scale structure   |
| Pelvic fin length   | PelvF   | Length from upper insertion point of fin to tip of longest branched ray  |
| Pectoral fin base   | PecFB   | Length between insertions of fin   |
| Pectoral fin 1 length                                       | PecF1   | Length from upper insertion point of fin to tip of unbranched ray  |
| Pectoral fin 2 length                                       | PecF2   | Length from upper insertion point of fin to tip of longest branched ray  |
| Dorsal fin base   | DFB     | Length between insertions of fin   |
| Length of anterior part of dorsal fin erected               | DFAe    | Length from anterior insertion point of fin to tip of longest unbranched ray, when fin is fully erected  |
| Length of anterior part of dorsal fin depressed             | DFAd    | Length from anterior insertion point of fin to tip of longest unbranched ray, when fin is depressed  |
| Length of posterior part of dorsal fin erected              | DFPe    | Length from posterior insertion point of fin to tip of most posterior branched ray, when fin is erected  |
| Anal fin base   | AFB     | Length between insertions of fin   |
| Length of anterior part of the anal fin                     | AFAe    | Length from anterior insertion point of fin to tip of longest branched ray, when fin is fully erected  |
| Adipose fin base  | AdFB    | Length between insertions of fin   |
| Caudal fin length   | CF      | Length from the middle of hypural plate of the caudal fin (internally this is the expanded bones at the end of the backbone that support the caudal fin, externally where the lateral line scales end) to the tip of the longest unbranched ray either being on the dorsal or ventral part of the caudal fin |
| Caudal peduncle depth                                       | CD      | Vertical distance between dorsal and ventral margins of the caudal peduncle at its narrowest part  |
| Caudal peduncle length                                      | CL      | Length from posterior insertion point of anal fin to the middle of the hypural plate of the caudal fin   |
| Length from anterior part of adipose fin to caudal fin base | PAc     | Length from anterior insertion point of adipose fin to the middle of the hypural plate of the caudal fin   |
| Dorsal head length  | DHL     | Length from tip of snout to most posterior part of the frontal head bone   |
| Prepelvic length  | PreP    | Length from tip of snout to anterior insertion point of pelvic fin   |
| Preanal length  | PreA    | Length from tip of snout to anterior insertion point of anal fin   |
| Standard length   | SL      | Length from tip of snout to the middle of the hypural plate of the caudal fin  |
| Total length  | TL      | Length from tip of snout to the tip of longest unbranched ray either being on the dorsal or ventral part of the caudal fin   |
| Predorsal length  | PreD    | Length from tip of snout to anterior insertion point of dorsal fin   |
| Body depth  | BD      | Vertical distance between dorsal and ventral margins of body from anterior insertion point of dorsal fin to anterior insertion of pelvic fin: not necessarily the greatest body depth  |
| Postdorsal length   | PostD   | Length from posterior insertion point of dorsal fin to middle of hypural plate of the caudal fin   |
| <b>Head</b>   |         |  |
| Eye diameter  | ED      | Horizontal distance across the midline of the eye from the anterior to the posterior margin of the soft eye tissue   |
| Eye cavity  | EC      | Horizontal distance across the midline of the eye from the anterior margin of the eye socket to the posterior margin of the eye cavity   |
| Eye height  | EH      | Vertical distance across the midline of the eye from the dorsal margin of the eye cavity to the ventral margin of the eye cavity   |
| Eye socket  | ES      | Horizontal distance from the anterior margin of the eye socket to the most anterior point of the the posterior margin of the eye socket  |
| Postorbital length  | PostO   | Length from posterior margin of the eye to the most posterior point of the operculum   |
| Head length   | HL      | Length from the tip of snout to most posterior point of the operculum margin   |
| Head depth  | HD      | The transverse distance between margins at the widest point of the head.   |
| Head width  | HW      | Distance between the posterior margins of the left and right operculum   |
| Mouth width   | MW      | The transverse distance between margins of the upper and lower jaw   |
| Upper jaw length  | UJ      | Length from the tip of the snout to most posterior point of the upper jaw  |
| Lower jaw length  | LJ      | Length from the most anterior point of the lower jaw to the lower jaw insertion  |
| Lower jaw width   | LJW     | Length between the anterior left and right side of the lower jaw   |
| Upper jaw width   | UJW     | Length between the posterior left and right point of the upper jaw   |
| Length of maxilla   | M       | Length from the most anterior point of the maxilla to the most posterior point of the maxilla  |

| Morphological characters  | Acronym | Description  |
|---------------------------|---------|--|
| Snout length              | SN      | Length from tip of snout to anterior margin of the eye   |
| Snouth depth              | SD      | Vertical distance from the upper to the lower margin of the rostral plate  |
| Snouth width              | SW      | Horizontal distance from the left to the right margin of the rostral plate   |
| Interorbital width        | IOW     | Distance between the anterior margin of the left and right eye cavity  |
| Internarial width         | INW     | Distance between the right and left nostrils   |
| <b>Gill</b>               |         |  |
| Upper arch length         | UA      | Length of the first hypobranchial (upper arch) from the most anterior point to the joint of the hypo- and ceratobranchial where the middle raker emerges   |
| Lower arch length         | LA      | Length of the first ceratobranchial (lower arch) from the most anterior point to the joint of the hypo- and ceratobranchial where the middle raker emerges |
| Middle gill raker length  | MGR     | Length of the gill raker directly at the joint of the the upper and lower first arch, from the insertion of the gill raker to the tip of the gill raker    |
| Longest gill raker length | LGR     | Length of the longest gill raker either on the upper and lower first arch, from the insertion of the gill raker to the tip of the gill raker               |

**Table 2.** Meristic characters, their acronyms and a brief description of each character.

| Mersitic characters          | Acronym  | Description  |
|------------------------------|----------|--|
| Pelvic fin rays              | PelvFR   | Number of unbranched and branched rays   |
| Pectoral fin rays            | PecFR    | Number of unbranched and branched rays   |
| Dorsal fin rays              | DFR      | Number of unbranched and branched rays; the posteriormost dorsal rays are often borne from a single pterygiophore (the bones on which the rays articulate), in such a case the two rays are accounted as 2 rays, rudimentary unbranched rays in front of the fin are counted |
| Anal fin rays                | AFR      | Number of unbranched and branched rays; the posteriormost anal rays are often borne from a single pterygiophore (the bones on which the rays articulate), in such a case the two rays are accounted as 2 rays, rudimentary unbranched rays in front of the fin are counted   |
| Lateral line scales          | LS       | Scales bearing the lateral-line column canal from the head to the end of the hypural plate of the caudal peduncle  |
| Predorsal scales             | PDS      | Dorsal scales starting from the posterior end of the head to the anterior insertion of the dorsal fin  |
| Transverse dorsal scales     | TDS      | "Number of scale rows between anterior insertion of the dorsal fin and the lateral line, not accounting for the lateral line scale and the scale on the dorsal midline (in front of the dorsal fin) "  |
| Transverse anal scales       | TAS      | "Number of scale rows between anterior insertion of the anal fin and the lateral line, not accounting for the lateral line scale and the scale on the ventral midline (in front of the anal fin) "   |
| Transverse pelvic scales     | TPS      | "Number of scale rows between anterior insertion of the pelvic fin and the lateral line, not accounting for the lateral line scale and the scale on the ventral midline (in front of the pelvic fin)"  |
| Upper arch gill raker number | UGR      | Number of gill rakers on first upper arch; all rakers including rudimentary developed rakers   |
| Lower arch gill raker number | LGR      | Number of gill rakers on first lower arch; all rakers including rudimentary developed rakers and the middle raker  |
| Total gill raker number      | total GR | Gill raker number of upper and lower arch combined   |

## Analysis of morphological data

The average sizes of fish from each species differ between lakes enough that for certain species such as for *C. abellus* the average size and the maximum size of adult fish of the population in Lake Brienz do not overlap with the average size and the minimum size of adult fish of the population in Lake Thun (Suppl. material 1: Figures S4–S6). The lakes differ naturally in several abiotic factors (max lake depth, bathymetric slope, average lake temperature, water turbidity; see Alexander et al. 2015) that may be related to the different growth rates of conspecific populations of several species and thus different size-at-age between the lakes (Kirchhofer 1995; Müller et al. 2007). Comparisons with multivariate statistical methods (PCA, LDA see below) are difficult in such cases, when size differences between populations or species are large and there is little to no overlap (Baur et al. 2014). We thus performed separate multivariate ratio analysis (see

below for details) on the species from lakes Thun and Brienz. In the Lake Thun dataset the partially allochthonous species *C. acrinus* was not included in the comparison between the types of the previously described species of *C. alpinus*, *C. albellus*, and *C. fatioi* (type locality Lake Thun) and the contemporary specimens, because the introduction of whitefish from Lake Constance, from which *C. acrinus* shares genetic ancestry contributions, postdates the collection year of the types. Furthermore, in Lake Brienz we divided the data into two subsets to avoid allometry issues; a subset containing individuals smaller than 163.5 mm SL and one subset containing individuals larger than 163.5 mm SL. This threshold was chosen to retain several small individuals of the three larger whitefish species, *C. alpinus*, *C. brienzi*, and *C. fatioi* for the analysis with all individuals of the small whitefish species *C. albellus*. All four species of Lake Brienz are represented in both subsets albeit unequally distributed.

Multivariate ratio analysis is a method that performs principal component analysis (PCA) and linear discriminant analysis (LDA) on morphological ratios (Baur and Leuenberger 2011; Baur et al. 2014). Analysis of morphological ratios are especially well suited in a taxonomic context (László et al. 2013). A scree plot was used to identify the number of PC-axes that should be retained and plotted. In most cases the first two PC axes were retained, and, in a few cases, the third PC axis was also retained. We thus use the first three axes to visualize shape variation between the species. The eigenvalues of the PC-axes and the loadings of each trait can be found in the Suppl. material 1: Tables S1–S4. We further plotted the scores of each PC-axis against isosize to investigate the contribution of allometry to individual shape PC-axes. Isosize is an isometric size axis defined as the geometric mean of all characters used in the PCA. We report the linear regression coefficient  $R$  as a metric of the contribution of allometry to each PC-axes (Baur and Leuenberger 2011) (Suppl. material 1: Tables S1–S4). If the relationship between size and shape is strong, then such PC-axes are not informative to distinguish species based on shape itself.

For the development of a species identification key we used LDA analysis on all characters together and on subsets of only head or only body characters for all contemporary specimens from lakes Thun and Brienz separately to calculate the first two ratios of characters that best separate each of the species in each lake. This method also allows to estimate the extent of shape change with size (i.e., the contribution of allometry to these ratios) which is given as  $\delta$  and describes how good shape discriminates in comparison to size (see Baur and Leuenberger 2011: Page 818, formula 14). In several pairwise species comparisons, we had more variables than individuals which will not allow to calculate the best LDA ratios. In such cases we used a subset of the variables to match the number of individuals. The variables that were retained in this subset were chosen such that possibly informative characters in each pairwise comparison were kept. All the comparisons with a subset of characters are marked in the table and the respective characters that were excluded are listed (Tables 10, 11). Due to large size differences between the species of Lake Brienz the LDA ratios were calculated with three different datasets; once each with individuals larger or smaller than 163.5 mm SL and once with the full-size ranges of all species. Ratios marked in the table with an asterisk (\*) have very little or no

overlap with other species and were thus used in the identification key and the species diagnoses. All analyses were performed in RStudio v1.0.143 (R Studio Team 2015).

## Genetics

Genetic analysis of ten microsatellite loci were used for the Bayesian clustering algorithm program STRUCTURE (Pritchard et al. 2000) to assign all contemporary specimens of lakes Thun and Brienz to the different whitefish species present in either lake. DNA was extracted from fin tissue using Chelex and Proteinase-K following the manufacturer's standard protocol. All individuals were genotyped at ten microsatellite loci that were combined into two multiplex sets: CoCl49, CoCl68, CoCl6, C2–157, CoCl61, CoCl45 and BWF-2, CoCl4, CoCl18, CoCl10 (Patton et al. 1997; Turgeon et al. 1999; Rogers et al. 2004). DNA fragments were resolved on an automated DNA sequencer (ABI 3130xl) and genotypes were determined with the software Gene Mapper (ver. 4.0) with the same scoring-panel as in Dönz et al. (2018). Individuals that had missing data at more than two loci were excluded from further analysis.

From the targeted spawning fisheries (each at one spawning site in lakes Thun and Brienz along a depth gradient) a total of 663 individuals from Lake Thun had complete genotypes, ten individuals had one missing locus, and four individuals had two missing loci. A total of 284 individuals from Lake Brienz had complete genotypes, eighteen individuals had one missing locus, and four individuals had two missing loci. These individuals were assigned to the different species using the program STRUCTURE with reference populations of each species deriving from the study by Dönz et al. (2018). A detailed description of the assignment procedure can be found in Dönz et al. (2018). In brief, Dönz et al. (2018) had a dataset comprising 2388 fish from both lakes with the same set of ten microsatellite loci and the same scoring-panel as in our study. To find the most likely number of genetic clusters (K), they conducted a hierarchical cluster analysis (Coulon et al. 2008; Roy et al. 2015) using the individual-based Bayesian clustering algorithm implemented in STRUCTURE (Pritchard et al. 2000). They determined the most likely K for the full dataset of 2388 individuals, then the most likely K within each of the data subsets suggested by the previous analysis, and so forth until all subsets supported a value of  $K = 1$ . To determine correspondence of genetic clusters to known species, they assessed how individuals from targeted samplings of known species were distributed among the clusters. They then chose the 50 individuals with highest assignment likelihood to the corresponding clusters at each previous step in the hierarchical analysis and designated them as a reference panel for the six clusters. Afterwards this method can be used to obtain individual genetic assignment proportions to the six clusters inferred in the hierarchical analysis.

We used the reference panel from Dönz et al. (2018) as reference populations and assigned all the individuals from our data set to the six species clusters with the function PopFlag in STRUCTURE. Subsets of 50 individuals out of the 973 genotyped individuals (from the depth gradient data set) were run in separate assignment runs to

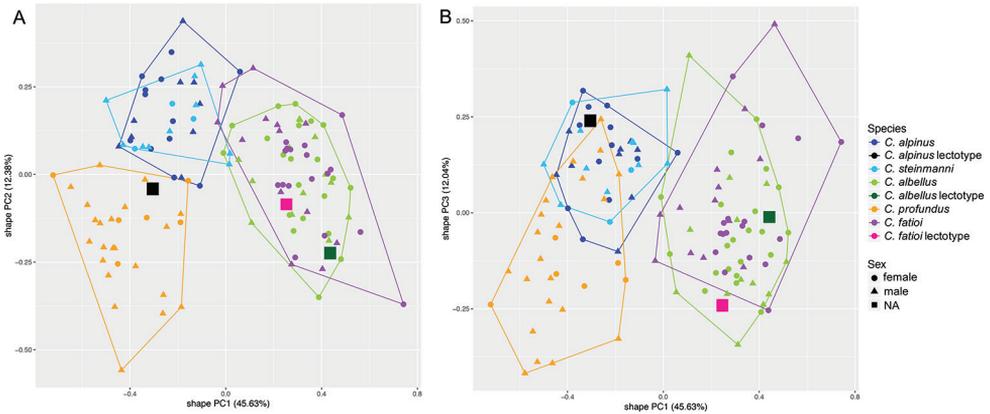
avoid issues with unequal sample sizes. For each of these analyses, we performed 10 replicates of  $K = 6$  with 200'000 burn-in steps and 200'000 MCMC steps using the admixture and correlated allele frequency model. We used Structure Harvester to generate input files for CLUMPP (ver. 1.1.2, Jakobsson and Rosenberg 2007), which we used to generate consensus percentages of assignment proportions from the 10 structure runs. We first retained all individuals with assignment probabilities higher than 70% to one cluster and chose among these individual's specimens for the taxonomic work (Dönz et al. 2018). This resulted in a total of 244 out of 677 (36%) individuals for Lake Thun and a total of 147 out of 296 (50%) individuals for Lake Brienz. We aimed at obtaining for each lake a total of ca. 20 specimens of each species for the taxonomic work. In cases where this number was not reached with specimens that had assignment probabilities higher than 70%, we supplemented the data set with individuals with lower assignment probabilities and checked if they cluster in morphospace with the respective specimens with higher assignment probabilities. A few additional specimens were taken from previous sampling campaigns, which were assigned by Dönz et al. (2018). We also took into consideration – next to the genetic species assignment – information regarding catch date and depth (reflecting spawning season and habitat). The percentage of assignment proportions for each contemporary specimen can be found together with all the other data underpinning the analyses reported in this paper in the online Dryad Data Repository (<http://doi.org/10.5061/dryad.pd2tq5g>).

Newer genomic findings by De-Kayne et al. (unpublished) suggest that whitefish from Lake Brienz, that have previously been assigned based on genetic analysis (see above; Dönz et al. 2018) to *C. steinmanni* and have also been selected based on these assignments for our taxonomic work, actually comprise of an endemic species in Lake Brienz, *C. brienzi*. The assignment probability to *C. steinmanni* of specimens of *C. brienzi*, which is based on the assignment method by Dönz et al. (2018), are for the sake of completeness still reported in the online dataset.

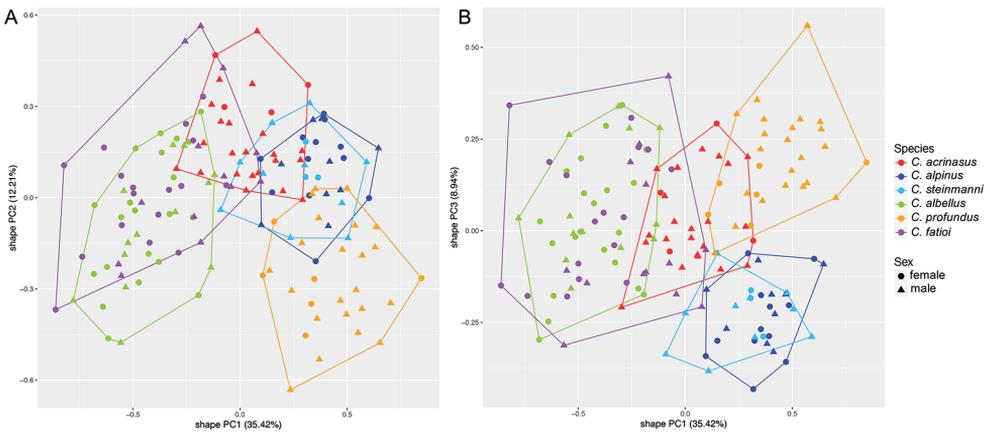
## Results

### Summary

The principal component analyses (shapePCA) on the morphological characters show that the type specimens of all previously described species *C. alpinus*, *C. albellus*, and *C. fatioi* group in morphospace within the ranges or adjacent to the ranges of the respective contemporary specimens of these species in Lake Thun (Figure 1a, b; Suppl. material 1: Figure S11a, b). The types of each of the three previously described species further mostly overlap within the ranges of each of the contemporary specimens of the three species from Lake Thun (Tables 3–5). We thus use the contemporary specimens of the previously described species *C. alpinus*, *C. albellus*, and *C. fatioi*, together with the holo- and paratypes of the newly described species *C. steinmanni*, *C. brienzi*, *C. profundus*, and *C. acrinus* to delineate the species. The shape PCA on

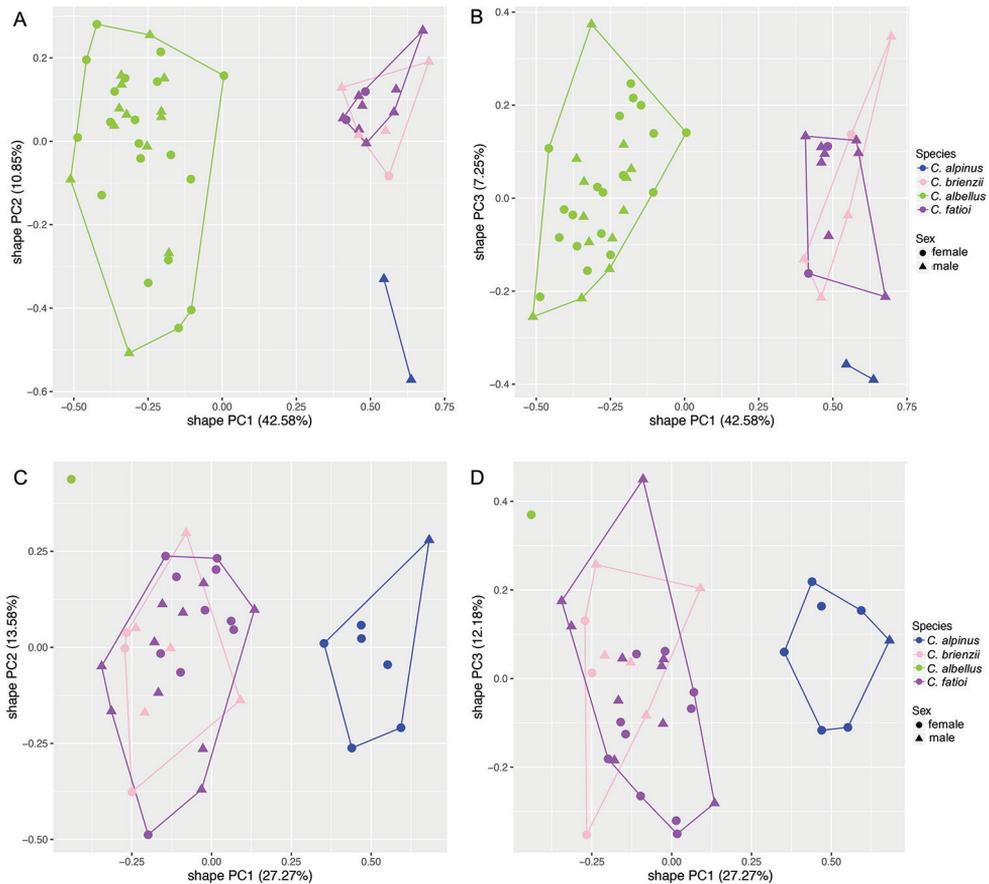


**Figure 1.** Principal Component Analysis showing that the types of the previously described species *C. alpinus*, *C. albellus* and *C. fatioi* (type locality: Lake Thun) lie within or adjacent to the ranges of the contemporary species of Lake Thun **A, B** shape PCA of the first vs. the second or third PC-axes explain together 70.05% of the variation in shape and are based on a subset (Suppl. material 1: Table S1) of 30 out of a total of 48 measured linear morphological characters (Table 1), since the type material lacked certain characters. Name-bearing types of the formerly described species are highlighted with enlarged symbols in the plots. The proportion of variance explained by each shape PC is given in brackets in the axis legend. PC-loadings and amount of shape variation explained by size are reported in Suppl. material 1: Table S1.



**Figure 2.** Principal Component Analysis showing the morphospace of the contemporary whitefish species *C. acrinus*, *C. alpinus*, *C. steinmanni*, *C. albellus*, *C. profundus* and *C. fatioi* from Lake Thun **A, B** shape PCA of the first vs. the second or third PC-axes explain together 56.5% of the variation in shape and are based on all 48 measured linear morphological characters (Table 1). The proportion of variance explained by each shape PC is given in brackets and the PC-loadings and amount of shape variation explained by size in Suppl. material 1: Table S2.

the contemporary specimens of Lake Thun shows three main clusters, one containing the species *C. alpinus* and *C. steinmanni*, one containing *C. albellus* and *C. fatioi*, and a third cluster with *C. profundus*, while *C. acrinus* lies intermediate between these three



**Figure 3.** Principal Component Analysis showing the morphospace of the contemporary whitefish species *C. alpinus*, *C. brienzi*, *C. albellus* and *C. fatioi* from Lake Brienz (**A–D**). **A, B** shape PCA of the first vs. the second or third PC-axes explain together 53–60.7% of the variation in shape and are based on all 48 measured linear morphological characters (Table 1), with a dataset containing specimens once smaller (**A, B**) and once larger (**C, D**) than 163.5 mm standard length (SL) to avoid allometry issues. The proportion of variance explained by each shape PC is given in brackets and the PC-loadings and amount of shape variation explained by size in Suppl. material 1: Table S3 (< 163.5 mm) and Suppl. material 1: Table S4 (> 163.5 mm).

clusters (Figure 2a, b). The shape PCA on the contemporary specimens of *C. alpinus*, *C. albellus*, *C. fatioi*, and *C. brienzi* of Lake Brienz reveals three clusters, one cluster containing *C. alpinus*, one containing *C. fatioi* and *C. brienzi*, and the third cluster containing *C. albellus* (Figure 3a–d). Some species cluster together in morphospace: In Lake Thun *C. steinmanni* groups with *C. alpinus* and *C. fatioi* with *C. albellus* and in Lake Brienz *C. brienzi* groups with *C. fatioi*. The species can be delineated further by several morphological and meristic characters as well as by morphological ratios extracted from linear discriminant analyses (Tables 3–11). *Coregonus acrinus* can also be distinguished from all four described Lake Constance whitefish species *C. wartmanni*, *C. macrophthalmus*, *C. arenicolus*, and *C. gutturosus* (Tables 9, 12).

## Species descriptions

### *Coregonus albellus* Fatio, 1890

#### Figure 4

*Coregonus exiguus albellus*: Fatio 1890

*Coregonus* “Brienzig”: Surbeck 1917; Steinmann 1950, Ruffi 1978, 1979; Kirchhofer and Tschumi 1986; Kirchhofer 1995; Bittner et al. 2010

*Coregonus* “Brienzig”, “Winterbrienzig”: Kirchhofer 1990; Kirchhofer 1995

*Coregonus* “Small type”: Maurer and Guthruf 2005; Müller et al. 2007

*Coregonus* sp. “winter spawning”: Kottelat and Freyhof 2007

*Coregonus* “Sommerbrienzig”, “BRI2”: Douglas et al. 1999; Douglas and Brunner 2002

*Coregonus* “Sommerbrienzig”, “THU5”: Douglas et al. 2003

*Coregonus* “Sommerbrienzig”, “Winterbrienzig”, “THU4”, “THU5”: Douglas and Brunner 2002

*Coregonus* sp. “Brienzig”: Vonlanthen and Périat 2013

*Coregonus* “Kropfer”: Heuscher 1901 (see also synonymy of *C. profundus*)

*Coregonus lavaretus* natio *arurensis*, oekot. *nanus*: Steinmann 1950

*Coregonus* “Zwergalbock”: Steinmann 1950

**Material examined. Lectotype.** MHNG-816.022, Switzerland, Lake Thun (46°40'N, 7°46'E), 165 mm SL, sex unknown.

**Non-types.** NMBE-1077186–1077202, NMBE-1077221–1077237, Switzerland, Lake Thun (46°40'N, 7°46'E), N = 34, 177–271 mm SL; NMBE-1059754; 1059768; 1059791; 1059801; 1059814, NMBE-1077129–1077131, NMBE-1077318–1077341, Switzerland, Lake Brienz (46°43'N, 7°57'E), N = 32, 101–164 mm SL.

**Diagnosis.** *Coregonus albellus* is a very small whitefish species in Lake Brienz and a small whitefish species in Lake Thun with weak pigmentation of all fins and body; the colouration on the flanks above the lateral line of specimens from Lake Thun are pale rose to brown and from Lake Brienz pale brown to light green; no or few small pigmented dots on the edge of the scales along the flank for specimens from Lake Thun and specimens from Lake Brienz sometimes have rather large pigmented dots more or less in a row on the upper dorsum; elongate slender body; large eye with a thin and roundish eye socket; tip of snout fleshy and roundish; many and long gill rakers.

**Differential diagnosis.** No single character was sufficient to distinguish *C. albellus* against all the five other species from Lake Thun and the species is diagnosed by a combination of characters. Based on ratios for the subset of whitefish from Lake Brienz smaller than 163.5 mm, *C. albellus* can be distinguished from the other three species from Lake Brienz by a smaller “postdorsal length / eye height” ratio (PostD/EH: 5.47–6.93 vs. 7.5–8.9). Also, when taking the full-size range (100–290 mm) of all species from Lake Brienz *C. albellus* can be distinguished from the three other species by a smaller “predorsal length / eye height” ratio (PreD/EH: 6.1–7.58 vs. 8.12–10.5) (Table 11).



**Figure 4.** *Coregonus albellus*, lakes Thun and Brienz, Switzerland **A** lectotype, MHNG-816.022, Lake Thun, 165 mm SL, sex unknown **B** non-type, Eawag-123825, Lake Thun, 221 mm SL, male **C** non-type, NMBE-1077320, Lake Brienz, 115.5 mm SL, male. The white scale (1cm) below each fish acts as a reference for the actual size of the specimen.

#### *Coregonus albellus*-*Coregonus alpinus*

The specimens from lakes Thun and Brienz of *C. albellus* differ from those of *C. alpinus* of both lakes in having a higher number of gill rakers (UGR#: 9–17, mode = 13 vs. 8–11, mode = 10; LGR#: 20–29, mode = 25 vs. 15–23, mode = 19; total GR: 32–44, mode = 38 vs. 25–34, mode = 29), a longer longest gill raker (14.1–21.8% HL, mean = 17.7 vs. 10–15.2% HL, mean = 11.9), a deeper adipose fin (4.5–9.2% SL, mean = 6.5 vs. 3.4–5.5% HL, mean = 4.4), a longer lower jaw (38.4–49.2% HL, mean = 43.6 vs. 33.8–41.4% HL, mean = 38.4) and a thinner eye socket (2–4.9% HL, mean = 3.4 vs. 3.3–6.3% HL, mean = 5).

**Table 3.** Morphological and meristic data of *C. albellus* Fatio, 1890 from lakes Thun and Brienz, MHNG-816.022 lectotype from Lake Thun; non-type material N = 34 from Lake Thun and N = 32 from Lake Brienz.

| Morpho-logical/characters     | <i>C. albellus</i><br>Lectotype | Both lakes           |             |              | Lake Thun     |            |                | Lake Brienz  |               |              |              |           |                |              |       |              |
|-------------------------------|---------------------------------|----------------------|-------------|--------------|---------------|------------|----------------|--------------|---------------|--------------|--------------|-----------|----------------|--------------|-------|--------------|
|                               |                                 | Non-types both sexes |             |              | Non-types     |            |                | Non-types    |               |              |              |           |                |              |       |              |
|                               |                                 | Mean ± StDev         | Range       | N-total = 66 | Mean ± StDev  | Range      | N-females = 21 | Mean ± StDev | Range         | N-males = 13 | Mean ± StDev | Range     | N-females = 19 | Mean ± StDev | Range | N-males = 13 |
| SL (mm)                       | 165.0                           | 173.2±51.9           | (101–271)   | 224.4±14.9   | (205–271)     | 216.6±18.1 | (177–254)      | 122.1±11.0   | (101–164)     | 122.9±13.5   | (101–164)    | 120.9±6.4 | (108–129)      |              |       |              |
| Percentage of standard length |                                 |                      |             |              |               |            |                |              |               |              |              |           |                |              |       |              |
| PelvFB                        | 3.6                             | 3.9±0.4              | (3.2–5.6)   | 4.0±0.3      | (3.4–4.7)     | 4.1±0.2    | (3.7–4.5)      | 3.8±0.5      | (3.2–5.6)     | 4.0±0.5      | (3.2–5.6)    | 3.6±0.2   | (3.3–4.0)      |              |       |              |
| PelvFS                        | na                              | 6.3±0.7              | (5.1–8.6)   | 6.2±0.7      | (5.1–7.3)     | 6.5±0.7    | (5.1–7.3)      | 6.4±0.7      | (5.5–8.6)     | 6.5±0.8      | (5.5–8.6)    | 6.3±0.6   | (5.7–7.8)      |              |       |              |
| PelvF                         | 14.1                            | 17.1±1.1             | (14.7–20.9) | 16.7±0.9     | (14.8–18.7)   | 17.1±1.1   | (14.8–18.7)    | 17.3±1.1     | (14.7–20.9)   | 17.5±1.4     | (14.7–20.9)  | 17.1±0.7  | (15.3–18.1)    |              |       |              |
| PecF1                         | 3.1                             | 3.3±0.3              | (2.7–4.8)   | 3.4±0.3      | (2.7–3.9)     | 3.5±0.2    | (2.9–3.9)      | 3.3±0.4      | (2.9–4.8)     | 3.5±0.5      | (3.0–4.8)    | 3.2±0.2   | (2.9–3.6)      |              |       |              |
| PecF1                         | na                              | 17.6±1.2             | (14.7–22.6) | 17.3±1.0     | (14.4–19.1)   | 17.4±1.1   | (14.7–18.8)    | 18.0±1.4     | (15.7–22.6)   | 18.2±1.5     | (15.7–22.6)  | 17.6±1.3  | (15.9–19.8)    |              |       |              |
| PecF2                         | na                              | 18.9±1.3             | (15.7–23.8) | 18.4±1.1     | (15.7–20.7)   | 18.2±1.1   | (16.4–20.1)    | 18.8±1.3     | (15.7–20.7)   | 19.4±1.3     | (16.9–23.8)  | 19.5±1.5  | (16.9–23.8)    |              |       |              |
| DfB                           | 11.7                            | 12.1±0.9             | (10.7–16.2) | 11.9±0.6     | (10.8–13.6)   | 12.0±0.7   | (11.0–13.6)    | 12.2±1.1     | (10.7–16.2)   | 12.6±1.2     | (10.8–16.2)  | 11.8±0.9  | (10.7–13.2)    |              |       |              |
| DfAe                          | na                              | 19.1±1.4             | (16.1–24.7) | 18.5±1.2     | (16.1–21.2)   | 18.3±0.9   | (16.1–19.6)    | 18.9±1.5     | (16.7–21.2)   | 19.7±1.5     | (17.3–24.7)  | 19.1±0.9  | (17.3–20.8)    |              |       |              |
| DfAd                          | na                              | 20.1±1.4             | (17.1–26.6) | 19.7±1.1     | (17.1–21.9)   | 19.5±0.9   | (17.3–21.4)    | 20.0±1.3     | (17.1–21.9)   | 20.6±1.5     | (18.3–26.6)  | 20.0±0.9  | (18.9–21.7)    |              |       |              |
| DfPe                          | 7                               | 5.4±0.7              | (3.7–7.2)   | 5.1±0.6      | (3.7–6.1)     | 5.0±0.5    | (3.7–5.9)      | 5.2±0.7      | (3.8–6.1)     | 5.7±0.7      | (4.4–7.2)    | 5.7±0.6   | (4.4–7.2)      |              |       |              |
| AfB                           | 13.1                            | 12.9±1               | (10.5–17)   | 12.7±0.8     | (11.1–14.9)   | 12.4±0.6   | (11.1–13.3)    | 13.1±0.8     | (12.0–14.9)   | 13.0±1.2     | (10.5–17.0)  | 13.3±1.3  | (11.5–17.0)    |              |       |              |
| AfAe                          | na                              | 12±0.9               | (9.7–14.4)  | 12.3±0.8     | (10.9–14.0)   | 12.0±0.7   | (10.9–13.4)    | 12.7±0.9     | (11.3–14.0)   | 11.7±1.0     | (9.7–14.4)   | 11.6±1.0  | (9.7–13.8)     |              |       |              |
| AdFB                          | 6.8                             | 6.5±1.1              | (4.5–9.2)   | 5.8±0.7      | (4.5–7.7)     | 5.8±0.7    | (4.7–6.8)      | 5.9±0.8      | (4.5–7.7)     | 7.2±1.1      | (4.5–9.2)    | 7.2±1.1   | (4.9–9.2)      |              |       |              |
| CF                            | na                              | 25±1.8               | (21.7–32.9) | 24±1.3       | (21.7–26.5)   | 23.8±1.1   | (21.7–26.4)    | 24.2±1.5     | (21.8–26.5)   | 26±1.8       | (24.4–32.9)  | 25.3±1.4  | (24–28.6)      |              |       |              |
| CD                            | 6.9                             | 7.2±0.5              | (6.3–10)    | 7.1±0.3      | (6.4–7.9)     | 7.1±0.4    | (6.4–7.9)      | 7.2±0.3      | (6.8–7.7)     | 7.3±0.6      | (6.3–10)     | 7.5±0.8   | (6.6–10)       |              |       |              |
| CL                            | 14.7                            | 13.3±0.8             | (11.7–16)   | 13.2±0.7     | (11.7–14.6)   | 13.2±0.7   | (11.7–14.5)    | 13.1±0.9     | (11.7–14.6)   | 13.5±0.9     | (12.1–16.0)  | 13.4±0.9  | (12.2–16.0)    |              |       |              |
| PdAC                          | 18.9                            | 19.8±1.5             | (16.9–24.2) | 18.9±1       | (16.9–20.9)   | 18.8±0.9   | (16.9–20.9)    | 19.3±0.9     | (17.3–20.4)   | 20.7±1.4     | (17.7–24.2)  | 20.5±1.8  | (17.7–24.2)    |              |       |              |
| DHL                           | 14.7                            | 16.4±1.8             | (14.1–23.1) | 15.0±0.7     | (14.1–16.5)   | 14.9±0.7   | (14.1–16.2)    | 15.2±0.4     | (14.1–16.5)   | 17.9±1.3     | (16.1–23.1)  | 18.3±1.4  | (16.8–23.1)    |              |       |              |
| PreP                          | 49.2                            | 51.9±2.4             | (48.4–67.7) | 52.0±1.6     | (49.5–56.0)   | 52.1±1.7   | (49.5–56.0)    | 51.9±1.4     | (49.5–54.3)   | 51.8±3.2     | (48.4–67.7)  | 52.2±3.9  | (49.1–67.7)    |              |       |              |
| PreA                          | 76.2                            | 77.1±3.1             | (74–100)    | 77.1±1.3     | (74.8–80.0)   | 77.2±1.2   | (75.2–79.7)    | 76.9±1.6     | (74.8–80.0)   | 77.2±4.3     | (74.0–100.0) | 77.7±5.5  | (74.8–100.0)   |              |       |              |
| PreD                          | 45.5                            | 47.2±2.2             | (43.1–61.2) | 46.5±1.1     | (43.1–48.4)   | 46.6±0.9   | (44.9–48.4)    | 46.2±1.1     | (43.0–47.7)   | 48±2.7       | (45.8–61.2)  | 48.5±3.3  | (45.8–61.2)    |              |       |              |
| BD                            | 25.2                            | 23.4±2.8             | (16.9–30.2) | 25.3±1.4     | (23.0–29.6)   | 25.5±1.5   | (23.5–29.6)    | 24.9±1.2     | (23.0–26.8)   | 21.4±2.5     | (16.9–30.2)  | 22.2±2.8  | (19.4–30.2)    |              |       |              |
| PostD                         | 43.8                            | 44.3±2               | (41.2–56.2) | 44.5±1.5     | (41.8–48.3)   | 44.6±1.4   | (41.8–46.6)    | 44.3±1.7     | (43.4–48.3)   | 44.1±2.5     | (41.2–56.2)  | 44.1±3.1  | (41.5–56.2)    |              |       |              |
| TL                            | na                              | 121.3±2.1            | (116.6–130) | 120.7±1.8    | (116.6–123.7) | 120.5±1.8  | (116.6–123.7)  | 121.1±1.8    | (118.4–123.7) | 122±2.2      | (118.2–130)  | 122.1±2.3 | (118.2–125.5)  |              |       |              |
| HL (mm)                       | 34.4                            | 38.4±8.8             | (26–51.9)   | 46.4±3.2     | (36.1–51.9)   | 46.6±2.8   | (41.5–51.9)    | 46.1±3.8     | (36.1–51.6)   | 29.9±2.5     | (26–39.2)    | 30.6±3    | (26–39.2)      |              |       |              |
| Percentage of head length     |                                 |                      |             |              |               |            |                |              |               |              |              |           |                |              |       |              |
| SN                            | 25.4                            | 22.8±2               | (18.7–27.2) | 24.2±1.3     | (20.9–27.2)   | 24.1±1.3   | (20.9–26.3)    | 24.4±1.3     | (22.5–27.2)   | 21.2±1.4     | (18.7–25.2)  | 21.3±1.2  | (19.7–23)      |              |       |              |
| ED                            | 23.5                            | 26.2±3.3             | (21.4–32)   | 23.4±1.3     | (21.4–25.9)   | 23.7±1.2   | (21.7–25.9)    | 22.9±1.3     | (21.4–25.3)   | 29.3±1.5     | (26.1–32)    | 29.4±1.7  | (26.1–32)      |              |       |              |



| Meristic characters | <i>C. albellus</i><br>Lectotype | Both lakes           |       | Lake Thun           |       |                       |           |                     |       | Lake Brienz           |       |                     |           |                       |       |                     |       |  |
|---------------------|---------------------------------|----------------------|-------|---------------------|-------|-----------------------|-----------|---------------------|-------|-----------------------|-------|---------------------|-----------|-----------------------|-------|---------------------|-------|--|
|                     |                                 | Non-types both sexes |       | Non-types           |       |                       | Non-types |                     |       | Non-types             |       |                     | Non-types |                       |       |                     |       |  |
|                     |                                 | <i>N-total</i> = 66  |       | <i>N-total</i> = 34 |       | <i>N-females</i> = 21 |           | <i>N-total</i> = 32 |       | <i>N-females</i> = 19 |       | <i>N-total</i> = 32 |           | <i>N-females</i> = 19 |       | <i>N-males</i> = 13 |       |  |
| Mode                | Range                           | Mode                 | Range | Mode                | Range | Mode                  | Range     | Mode                | Range | Mode                  | Range | Mode                | Range     | Mode                  | Range | Mode                | Range |  |
| AF unbranched       | 3                               | (2–4)                | 3     | (2–4)               | 3     | (2–4)                 | 3         | (2–4)               | 4     | (3–4)                 | 4     | (3–4)               | 4         | (3–4)                 | 4     | (3–4)               |       |  |
| AF branched         | 14                              | (10–14)              | 12    | (10–13)             | 12    | (10–13)               | 12        | (11–13)             | 12    | (10–14)               | 12    | (11–14)             | 12        | (10–14)               | 12    | (10–14)             |       |  |
| LS                  | 75                              | (70–86)              | 79    | (73–86)             | 79    | (73–83)               | 77        | (76–86)             | 76    | (70–84)               | 77    | (70–80)             | 78        | (70–84)               |       |                     |       |  |
| PDS                 | na                              | (26–37)              | 34    | (29–37)             | 34    | (29–37)               | 34        | (30–37)             | 31    | (26–35)               | 32    | (30–35)             | 31        | (26–34)               |       |                     |       |  |
| TDS                 | 9                               | (7–10)               | 9     | (8–10)              | 9     | (8–10)                | 9         | (9–10)              | 8     | (7–9)                 | 8     | (7–9)               | 8         | (7–9)                 |       |                     |       |  |
| TAS                 | 7                               | (6–9)                | 8     | (7–9)               | 8     | (7–9)                 | 8         | (8–9)               | 7     | (6–8)                 | 7     | (6–8)               | 8         | (6–8)                 |       |                     |       |  |
| TPS                 | 8                               | (7–9)                | 9     | (8–9)               | 9     | (8–9)                 | 9         | (8–9)               | 8     | (7–9)                 | 8     | (7–9)               | 8         | (7–8)                 |       |                     |       |  |
| UGR                 | 11                              | (9–17)               | 13    | (9–17)              | 13    | (9–15)                | 14        | (11–17)             | 13    | (11–16)               | 13    | (11–16)             | 13        | (12–14)               |       |                     |       |  |
| LGR                 | 23                              | (20–29)              | 24    | (20–28)             | 24    | (20–28)               | 26        | (22–27)             | 25    | (22–29)               | 25    | (22–29)             | 27        | (24–28)               |       |                     |       |  |
| total GR            | 34                              | (32–44)              | 38    | (32–44)             | 37    | (32–42)               | 38        | (33–44)             | 40    | (35–42)               | 38    | (35–42)             | 40        | (37–42)               |       |                     |       |  |

In Lake Brienz *C. albellus* further differs from *C. alpinus* by having translucent pelvic and anal fins compared to the moderately to strongly pigmented pelvic and anal fins of *C. alpinus*, a longer pectoral fin (Pectoral fin 1 length: 15.7–22.6% SL, mean = 18 vs. 13.9–17.9% SL, mean = 16.3; Pectoral fin 2 length: 16.9–23.8% SL, mean = 19.4 vs. 14.4–17.7% SL, mean = 16.9), a longer distance from the anal fin to the hypural plate of the caudal peduncle (17.7–24.2% SL, mean = 20.7 vs. 15.3–19.5% SL, mean = 17.6), a longer head (16.1–23.1% SL, mean = 17.9 vs. 14–16.3% SL, mean = 15.4), a larger eye and eye cavity (eye diameter: 26.1–32% HL, mean = 29.3 vs. 21.8–27.2% HL, mean = 24.3; eye height: 26.5–30.6% HL, mean = 28.7 vs. 22.4–27.1% HL, mean = 23.9; eye cavity: 30.4–36.8% HL, mean = 33.3 vs. 26.4–31.5% HL, mean = 29), and a longer upper jaw (28.6–34.9% HL, mean = 32.1 vs. 25.4–29.1% HL, mean = 26.8). Finally, *C. albellus* smaller than 163.5 mm SL can be distinguished from *C. alpinus* by a smaller “preanal length / lower jaw” ratio (PreA/LJ: 6.33–7.44 vs. 9.24–9.97) and a larger “pectoral fin 2 length / length of the depressed anterior part of the dorsal fin” ratio (PecF2/DFAd: 0.81–1.06 vs. 0.78–0.8). With the full size range of Lake Brienz specimens, *C. albellus* can be distinguished from *C. alpinus* by the smaller “predorsal length / lower jaw” ratio (PreD/LJ: 3.99–4.68 vs. 5.6–6.81), “erected anterior part of the dorsal fin / upper jaw” ratio (DFAe/UJ: 2.14–2.79 vs. 3.25–4.1), “head depth / upper jaw” (HD/UJ: 1.87–2.2 vs. 2.38–2.78) and a larger “lower jaw / interorbital width” ratio (LJ/IOW: 1.53–1.99 vs. 1.33–1.57). (Tables 3, 4, 11).

In Lake Thun *C. albellus* can further be distinguished from *C. alpinus* by having a less deep caudal peduncle (6.4–7.9% SL, mean = 7.1 vs. 7.6–8.9% SL, mean = 8.2) and a longer upper jaw (28.8–34.7% HL, mean = 31.2 vs. 24.3–30.1% HL, mean = 27.7). Based on pigmentation of the fins *C. albellus* can be distinguished from *C. alpinus* from Lake Thun by having translucent to weakly pigmented fins compared to strongly pigmented fins, respectively. In Lake Thun *C. albellus* can further be distinguished from *C. alpinus* by the smaller “caudal peduncle depth / upper jaw length” ratio (CD/UJ: 0.96–1.29 vs. 1.36–1.65) and “caudal peduncle depth / dorsal head length” ratio (CD/DHL: 0.44–0.54 vs. 0.54–0.62) (Tables 3, 4, 10).

#### ***Coregonus albellus*-*Coregonus fatioi***

In Lake Brienz *C. albellus* can be distinguished from *C. fatioi* by having a larger head (16.1–23% SL, mean = 17.9, vs. 14.5–16.8% SL, mean = 15.7), a larger eye and eye cavity (eye diameter: 26.1–32% HL, mean = 29.4 vs. 21.2–27.6% HL, mean = 24.8; eye cavity: 30.4–36.8% HL, mean = 33.3 vs. 25.3–33% HL, mean = 29; eye height: 26.5–30.6% HL, mean = 28.7 vs. 22.1–26.3% HL, mean = 24.4), a longer maxilla (22.6–26.9% HL, mean = 24.7 vs. 18.7–24.2% HL, mean = 21.7) and longer gill rakers (middle gill raker: 13.7–19.4% HL, mean = 16.5 vs. 10.5–15% HL, mean = 13.2; longest gill raker: 14.9–21.8% HL, mean = 18.2 vs. 12.3–16.4% HL, mean = 14.3). Based on ratios *C. albellus* smaller than 163.5 mm SL can be distinguished from *C. fatioi* by a larger “pectoral fin 2 length / preanal length” ratio (PecF2/PreA: 0.22–0.28 vs. 0.2–0.22), “upper jaw length / eye socket width” ratio (UJ/ES: 6.81–12.42 vs. 4.51–6.15) and “eye socket width / head length” ratio (ES/HL: 0.27–0.31 vs. 0.23–0.27). With the full-size range of Lake Brienz specimens (100–290 mm), *C. albellus*

can be distinguished from *C. fatioi* by a smaller “prepelvic length / eye height” ratio (PreP/EH: 6.56–7.98 vs. 8.94–11.43) (Tables 3, 5, 11).

In Lake Thun *C. albellus* can be distinguished from *C. fatioi* by its live colouration above the lateral line on the dorsum ranging from a pale rose to a pale brown compared to a light to dark green colouration in *C. fatioi*. *C. albellus* can further be differentiated from *C. fatioi* by having no or few small pigmented dots on the edge of the scales or on the boundary of two scales on the flank and dorsum compared to moderate or many dots on the flanks and dorsum in *C. fatioi*.

#### ***Coregonus albellus*-*Coregonus brienzii***

*Coregonus albellus* from Lake Brienz differs from *C. brienzii* by having a longer longest gill raker (14.9–21.8% HL, mean = 18.2 vs. 12.1–16.8% HL, mean = 14.7), a longer maxilla (22.6–26.9% HL, mean = 24.7 vs. 15.4–24% HL, mean = 21), anterior a longer dorsal fin (anterior dorsal fin erected: 17.3–24.7% SL, mean = 19.7 vs. 15.5–19.8% SL, mean = 17.9; anterior dorsal fin depressed: 18.3–26.6% SL, mean = 20.6 vs. 15.3–20.8% SL, mean = 18.6), a longer head (16.1–23.1% SL, mean = 17.9 vs. 14.6–16.8% SL, mean = 15.6) and a larger eye and eye cavity (eye diameter: 26.1–32% HL, mean = 29.3 vs. 23.1–28.3% HL, mean = 25.3; eye height: 26.5–30.6% HL, mean = 28.7 vs. 22–27.2% HL, mean = 24.4; eye cavity: 30.4–36.8% HL, mean = 33.3 vs. 25.6–32.9% HL, mean = 29). Based on ratios *C. albellus* smaller than 163.5 mm SL can be distinguished from *C. brienzii* by a larger “maxilla length / eye socket width” ratio (M/ES: 5.35–9.76 vs. 3.31–4.37), “pectoral fin 2 length / predorsal length” ratio (PecF2/PreD: 0.36–0.45 vs. 0.29–0.32), “lower jaw length / eye socket width” ratio (LJ/ES: 9.62–17.28 vs. 6.01–6.49) and a smaller “predorsal length / lower jaw length” ratio (PreD/LJ: 3.99–4.68 vs. 5.05–5.57). With the full size range (100–290 mm) of Lake Brienz specimens, *C. albellus* can be distinguished from *C. brienzii* by a larger “eye height / head length” ratio (EH/HL: 0.27–0.31 vs. 0.22–0.27) and a smaller “predorsal length / eye height” ratio (PreD/EH: 6.1–7.58 vs. 8.12–10.32) (Tables 3, 7, 11).

#### ***Coregonus albellus*-*Coregonus steinmanni***

*Coregonus albellus* from Lake Thun can be distinguished from *C. steinmanni* by having a longer longest gill raker (14.1–20.3% HL, mean = 17.2 vs. 10–14.4% HL, mean = 12.1), a longer maxilla (20.1–26.8% HL, mean = 22.4 vs. 18.1–21.8% HL, mean = 19.7), a less deep caudal peduncle (6.4–7.9% SL, mean = 7.1 vs. 7.5–8.6% SL, mean = 8.0) and a deeper adipose fin (4.5–7.7% SL, mean = 5.8 vs. 3.7–5.4% HL, mean = 4.5). Based on ratios *C. albellus* can be distinguished from *C. steinmanni* by a smaller “caudal peduncle depth / upper jaw length” ratio (CD/UJ: 0.96–1.29 vs. 1.36–1.55) (Tables 3, 6, 10).

#### ***Coregonus albellus*-*Coregonus profundus***

*Coregonus albellus* from Lake Thun differs from *C. profundus* by having more and longer gill rakers (upper arch gill raker number: 9–17, mode = 13 vs. 5–10, mode = 9; lower arch gill raker number: 20–28, mode = 24 vs. 10–18, mode = 14; total number of gill rakers: 32–44, mode = 38 vs. 15–27, mode = 21; middle gill raker length: 11.7–18.3% HL, mean = 15.6 vs. 7.6–11.7% HL, mean = 9.2; longest gill raker length:

14.1–20.3% HL, mean = 17.2 vs. 7.8–12.4% HL, mean = 10.1). Based on ratios *C. albellus* can be distinguished from *C. profundus* by a larger “caudal peduncle length / eye cavity length” ratio (CL/EC: 1.97–2.87 vs. 1.56–2.09) (Tables 3, 8, 10).

***Coregonus albellus*-*Coregonus acrinus***

*Coregonus albellus* from Thun can be distinguished from *C. acrinus* by having a deeper adipose fin (4.5–7.7% SL, mean = 5.8 vs. 3.7–6.2% SL, mean = 4.7), a thinner eye socket (ES: 2–4.9% HL, mean = 3.2 vs. 3.2–6.4% HL, mean = 4.7) and a longer longest gill raker (14.1–20.3% HL, mean = 17.2 vs. 11.4–16.9% HL, mean = 14.5) (Tables 3, 9).

**Description.** General appearance is shown in Figure 4. Morphological and meristic characters of both sexes can be found in Table 3 and Suppl. material 1: Table S6 and first- and second-best ratios for both sexes combined can be found in Tables 10, 11. The description is valid for both sexes and both lakes; differences between the populations of lakes Thun and Brienz are mentioned.

**Shape:** Body elongate, slender. Greatest body depth anterior of the dorsal fin. Ventral profile and dorsal profile similar and slightly arched. Dorsal and ventral profile from tip of snout to interorbital mostly straight and then slightly convex to dorsal and pelvic fin origin respectively. Head long. Snout often 40–50° angle to the body axis anterior of the eye, such that the profile from the tip of the snout to the vertical projection where the anterior part of the eye crosses the dorsal profile is straight and afterwards slightly convex. Mouth (i.e., width of upper and lower jaw) wide, long and often terminal and only rarely slightly sub-terminal. Snout mostly wider than deep, not strongly pronounced, since the tip of the snout is often fleshy and roundish. Large eye, which is more pronounced in specimens from Lake Brienz. Individuals from both lakes have a thin and roundish eye-socket from the middle to the outer margins. Pectoral fin long and moderately tapered. Anterior unbranched ray of the erected dorsal fin range from almost vertically straight to an approx. 70–80° angle to body axis and only bent slightly posteriorly at the end of the ray. Caudal peduncle narrow and elongated with caudal fin forked and sometimes moderately to strongly asymmetrical with either the ventral or dorsal part being longer. Unbranched ray of anal fin straight and rarely bent posteriorly at the end of the ray. Anal fin longest anteriorly and progressively shortening posteriorly with the outer margin of the anal fin slightly concave.

**Meristics:** Many and long gill rakers.

**Colour:** Pigmentation of fins and body overall weak in live specimens. In specimens from Lake Thun the pectoral fin is translucent, sometimes yellowish with faint pigmentation at the median to distal parts of the fin. Pelvic fin is translucent and only weakly to moderately pigmented. Dorsal, adipose, anal and caudal fins are moderately pigmented. In specimens from Lake Brienz all fins are translucent, with the dorsal, anal and caudal fins sometimes showing some very faint pigmentation. In both lakes fish have a silvery appearance along the flanks and dorsally above the lateral line the silvery appearance changes to a pale rose colouration (e.g., RGB (247, 187, 175)) and then to a pale brown (e.g., RGB (230, 202, 110)). In specimens from Lake Thun the flanks very rarely have few pigmented small dots on the scales. Distribution of dots are bound

to the scale patterning (i.e., at the edge of the scales or at the boundary point of two scales. In specimens from Lake Brienz the upper dorsum ranges from pale brown (e.g., RGB (230, 202, 110)) to a light green colouration (e.g., RGB (136, 245, 205)) and sometimes has pigmented dots more or less in a row on the upper dorsum that are rather large (“cheetah look”) (Suppl. material 1: Figure S7). Distribution of the dots not restricted to the scale patterning (i.e., at the edge of the scales or at the boundary point of two scales), as can be found for the species of *C. alpinus*, *C. steinmanni*, *C. brienzii* and *C. fatioi*. For a comparison to the main colouration found in the other species see Suppl. material 1: Figure S8. Dorsal part of head of specimens of Lake Brienz is weakly pigmented, whereas that of specimens from Lake Thun is moderately pigmented. Snout around the nostrils is weakly (Lake Brienz) to moderately (Lake Thun) pigmented with a gap of little pigmentation posteriorly of the nostrils up to the height of the middle of the eyes. Operculum and pre-operculum are silvery with one black dot on the lower margin of the pre-operculum. Preserved specimens are pale in colouration with similar pigmentation as described for live specimens. The silvery, translucent, not coloured or unpigmented parts of the body become brown-yellowish (e.g., RGB (239, 210, 40)), whereas the pigmented parts are conserved and the coloured parts (dorsally above the lateral line) become brownish (e.g., RGB (186, 140, 100)).

**Distribution and notes on biology.** *Coregonus albellus* is found in the lakes Thun (46°40'N, 7°46'E) and Brienz (46°43'N, 7°57'E) that are connected by the short river Böödeli Aare at Interlaken. It is believed to have been endemic to these lakes yet, individual fish have been caught in Lake Biel (47°05'N, 7°10'E) in recent years (since 2005), after it was artificially connected with Lake Thun through the river Aare during the Jura water correction project dating back to 1868–1878. Individuals of *C. albellus* were first identified by local fishermen and fisherwomen, which reported that they had caught small, ripe fish during the summer months (Bittner 2009). The native whitefish species of Lake Biel only spawn in the winter months (Fatio 1885; Steinmann 1950; Ruffi 1978). Genetic analysis has shown that these summer-ripe individuals belong to the species *C. albellus* (Bittner 2009). We show for two ripe specimens caught in summer in Lake Biel, genetically assigned based on the assignment method of Dönz et al. (2018) to *C. albellus* with 84% and 94% probability, that they can also be assigned to *C. albellus* based on their morphology (gill raker number, morphological characters) (Suppl. material 1: Figure S9). The species may have established an independent population in Lake Biel, since ripe fish have now been caught for several years in reasonable numbers during the usual spawning period known for this species from Lake Thun (Bittner 2009; Vonlanthen and Périat 2018). *Coregonus albellus* feeds predominantly on zooplankton (stomach content for Lake Brienz: Maurer and Guthruff 2005; Müller et al. 2007; isotopic signature for both lakes: Selz 2008; Hudson 2011; Ingram et al. 2012) and has a slow growth rate (Kirchhofer 1995; Müller et al. 2007; Bittner et al. unpublished). The gill raker number and length of *C. albellus* (many and long gill rakers) also suggests that, based on the functional properties of the number of gill rakers (experimentally tested with specimens of this species and other whitefish species from lakes Thun and Lucerne) (Lundsgaard-Hansen et al. 2013; Roesch

et al. 2013), that *C. albellus* feeds predominantly on zooplankton. Habitat-stratified random sampling of lakes Thun (mid-October 2013: Vonlanthen et al. 2015) and Brienz (mid-September 2011: Vonlanthen et al. 2013) show for a snapshot of a few months in summer, that *C. albellus* in Lake Thun occupies the moderately shallow to the deepest benthic waters (approx. 30–217 m;  $N = 29$ ) and the moderately shallow to moderately deep pelagic waters (approx. 10–70 m;  $N = 44$ ) (Dönz et al. 2018). In Lake Brienz *C. albellus* occupies the very shallow (few meters) to the deepest waters (260 m) of the benthic habitat ( $N = 78$ ) and the very shallow to the deeper waters of the pelagic habitat (few meters down to approx. 60 m and exceptionally down to 130 m;  $N = 47$ ) (Dönz et al. 2018). It is to note that the habitat-stratified random sampling data for both lakes only covers a short period of time (one month in late summer) and it is thus not clear how the species are distributed spatially through the rest of the year. Furthermore, the habitat-stratified random sampling in both lakes did not distinguish between ripe and unripe specimens, and thus in the case of *C. albellus* the distribution pattern along the depth in the benthic zone is biased by the spawning aggregation of this species since the sampling period in both lakes coincides with the main spawning season of this species. Most of the whitefish that were phenotypically assigned as *C. albellus* and that were caught in deeper waters during habitat stratified sampling of lakes Brienz and Thun were ripe (PV pers. obs.). In Lake Thun *C. albellus* phenotypically resembles *C. fatioi* and to some extent *C. profundus*. Interestingly, Steinmann (1950) already mentioned for Lake Thun that *C. albellus* (Steinmann, 1950: *Coregonus lavaretus* L. nat. *arurenis*, oekot. *nanus*; common name: “Zwergalbock” or “Brienzlig”) resembles morphologically *C. fatioi* (Steinmann, 1950: *Coregonus lavaretus* L. nat. *arurenis*, oekot. *pelagicus*; common name: “Schwebalbock” or “Albock”). The average size (total length) at 3 years of age for specimens in this study is  $258 \pm 13$  mm (mean and standard deviation,  $N = 9$ ) and  $152 \pm 8$  mm ( $N = 14$ ) for lakes Thun and Brienz, respectively (Suppl. material 1: Figures S4–S6). In Lake Brienz the size of 3-year old specimens of *C. albellus* is considerably smaller than that of the other three whitefish species (*C. alpinus*, *C. brienzi*, *C. fatioi*), whereas in Lake Thun it is similar to that of *C. profundus* and *C. fatioi* (Suppl. material 1: Figure S6) and smaller than that of *C. alpinus*, *C. steinmanni*, and *C. acrinus*. *Coregonus albellus* has a long spawning season with two peaks. The main spawning peak is in late summer/early autumn from August to October (Locally known as “Sommer-Brienzlig”) and the second peak is in early to late winter from December to March (locally known as “Winter-Brienzlig”) (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). Spawning depth varies with spawning season and can range from approx. 30 m to max. lake depth at 217 m in Lake Thun and approx. 50 m to max. lake depth at 261 m in Lake Brienz (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). The spawning season and depth of *C. albellus* partially overlaps with that of *C. steinmanni*, *C. fatioi*, and *C. profundus* in Lake Thun and with that of *C. brienzi* and *C. fatioi* in Lake Brienz.

**Common names.** Brienzlig, Brienzling; often the time of the year the fish is caught on the spawning grounds is added to the name and shows that this species has a very wide spawning season: Sommer-Brienzlig (for summer) or Winter-Brienzlig (for win-

ter). This species was historically known by local fishermen and fisherwomen as white whitefish (German: “Weissfelchen”, but also Albele and Albuli). The common name for this species today is Brienzing which has an ending that is known as a diminutive suffix.

### ***Coregonus alpinus* Fatio, 1885**

#### **Figure 5**

*Coregonus* “Albock”: Ruffi 1978, 1979; Kirchhofer and Tschumi 1986; Kirchhofer 1995 (see also synonymy of *C. steinmanni* and *C. acrinasus*)

*Coregonus balleus*: Fatio 1885

*Coregonus* “Balchen”, “THU2”: Douglas et al. 1999, 2003; Douglas and Brunner 2002 (see also synonymy of *C. steinmanni*)

*Coregonus* “Balchen”: Heuscher 1901; Surbeck 1917 (see also synonymy of *C. steinmanni*)

*Coregonus* “Felchen”: Kirchhofer 1990; Kirchhofer 1995 (see also synonymy of *C. fatioi* and *C. brienzi*)

*Coregonus* “Large type”: Maurer and Guthruf 2005; Müller et al. 2007 (see also synonymy of *C. fatioi* and *C. brienzi*)

*Coregonus lavaretus* natio *arurensis*, oekot. *litoralis*: Steinmann 1950

*Coregonus lavaretus* natio *arurensis*, oekot. *primigenius*: Steinmann 1950 (see also synonymy of *C. fatioi* and *C. steinmanni*)

*Coregonus schinzii alpinus*: Fatio 1885

*Coregonus schinzii helveticus*: Fatio 1890

*Coregonus schinzii helveticus* var. *Thunensis*: Fatio 1890

*Coregonus* sp. “Balchen”: Hudson et al. 2011, 2013, 2016; Ingram et al. 2012; Vonlanthen et al. 2012, 2015; Lundsgaard-Hansen et al. 2013; Roesch et al. 2013; Vonlanthen and Périat 2013 (see also synonymy of *C. steinmanni* and *C. brienzi*)

*Coregonus* sp. “Balchen 1”: Dönz et al. 2018

*Coregonus* “Albock”, “Uferalbock”: Steinmann 1950 (see also synonymy of *C. steinmanni* and *C. fatioi*)

**Material examined. Lectotype.** MHNG-717.045, Switzerland, Lake Thun (46°40'N, 7°46'E), 283 mm SL, sex unknown.

**Non-types.** NMBE-1077241–1077261, Switzerland, Lake Thun (46°40'N, 7°46'E), N = 21, 210–364 mm SL; NMBE-1059817; 1059821; 1077134, NMBE-1077110–1077115, Switzerland, Lake Brienz (46°43'N, 7°57'E), N = 9, 147–290 mm SL.

**Diagnosis.** *Coregonus alpinus* is a large whitefish with strong pigmentation of all fins and the body; greenish blue colour on the flanks above the lateral line; moderate to many pigmented small dots on the scales along the flank and the dorsum; deep bodied; truncated blunt snout; short head; sub-terminal mouth; small eye with a thick and triangular-shaped eye socket; short and stout caudal peduncle; few and short gill rakers.

**Differential diagnosis.** Differential diagnosis against *C. albellus* is given under that species account. The total number of gill rakers of 25 to 34 with mode-values

of 28, 29, and 30 distinguishes *C. alpinus* from all other six whitefish species of lakes Thun and Brienz, by either having more gill rakers than the species *C. profundus* (total GR: 15–27, mode = 21) or fewer gill rakers than *C. fatioi* (total GR: 32–43, mode = 38), *C. albellus* (32–44, mode = 38), *C. steinmanni* (30–35, mode = 31), *C. brienzi* (32–39, mode = 37) and *C. acrinus* (30–40, mode = 36) (Suppl. material 1: Table S6). The contemporary gill raker range is congruent with the historical gill raker range (23–27) given in Fatio (1890).

For specimens in Lake Brienz smaller than 163.5 mm SL *C. alpinus* can be distinguished from the other three whitefish species by a larger “length of the depressed anterior part of the dorsal fin / lower jaw length” ratio (DFA<sub>d</sub>/LJ: 2.57–2.58 vs. 1.6–2.1). For fish larger than 163.5 mm SL, *C. alpinus* can be distinguished from *C. brienzi* and *C. fatioi* by a larger “length of the erected anterior part of the dorsal fin / upper jaw length” ratio (DFA<sub>e</sub>/UJ: 3.28–4.1 vs. 2.58–3.19). With the full-size range (100–290 mm) of Lake Brienz specimens, *C. alpinus* can be distinguished from the other three whitefish species by a larger “length of the erected anterior part of the dorsal fin / upper jaw length” ratio (DFA<sub>e</sub>/UJ: 3.25–4.1 vs. 2.14–3.19) (Table 11).

#### ***Coregonus alpinus*-*Coregonus fatioi***

The specimens from lakes Thun and Brienz of *C. alpinus* can be distinguished from those of *C. fatioi* by having a shorter under jaw (24.3–30.1% HL, mean = 27.4 vs. 27.6–34.1% HL, mean = 30), and a shorter longest gill raker (10–15.2% HL, mean = 11.9 vs. 12.3–22.6, mean = 15.6).

In Lake Brienz *C. alpinus* can be distinguished from *C. fatioi* by having a shorter caudal peduncle (11.3–13.9% SL, mean = 12.5 vs. 13.1–16.1% SL, mean = 14.2) and a shorter and narrower lower jaw (lower jaw length: 33.8–39.4% HL, mean = 38.2 vs. 37.6–48.4% HL, mean = 42.6; lower jaw width: 7.3–10.6% HL, mean = 8.8 vs. 8.6–13.3% HL, mean = 11.6). For fish from Lake Brienz larger than 163.5 mm SL, *C. alpinus* can be distinguished based on ratios from *C. fatioi* by having a larger “length of the erected anterior part of the anal fin / upper jaw length” ratio (AFA<sub>e</sub>/UJ: 1.96–2.5 vs. 1.66–1.96) and a larger “head length / upper jaw length” ratio (HL/UJ: 3.55–3.93 vs. 3.13–3.55). With the full size range (100–290 mm) of Lake Brienz specimens, *C. alpinus* can be distinguished from *C. fatioi* by having a larger “length of the erected anterior part of the dorsal fin / upper jaw length” ratio (DFA<sub>e</sub>/UJ: 3.25–4.1 vs. 2.14–3.19) (Table 11).

In Lake Thun *C. alpinus* can be further distinguished from *C. fatioi* by having a shorter postdorsal length (38.3–43.9% SL, mean = 42.7 vs. 41.6–50.7% SL, mean = 44.9) and a thicker eye socket (3.4–6.3% HL, mean = 5.1 vs. 1.7–5.9% HL, mean = 3.6). Based on ratios *C. alpinus* can be distinguished from *C. fatioi* by having a larger “caudal peduncle depth / postdorsal length” ratio (CD/PostD: 0.17–0.21 vs. 0.14–0.17) (Tables 4, 5, 10).

#### ***Coregonus alpinus*-*Coregonus brienzi***

*C. alpinus* from Lake Brienz can be differentiated from *C. brienzi* by having a shorter caudal peduncle (11.3–13.9% SL, mean = 12.5 vs. 12.2–15.8% SL, mean = 13.8), a shorter upper and lower jaw (upper jaw: 25.4–29.1% HL, mean = 26.8 vs. 27.1–32% HL, mean = 29.5; lower jaw: 33.8–39.4% HL, mean = 38.2 vs. 40.5–45.7%

**Table 4.** Morphological and meristic data of *C. alpinus* Fatio 1885 from lakes Thun and Brienz, MHNG-717.045 lectotype from Lake Thun; non-type material N = 21 from Lake Thun and N = 9 from Lake Brienz.

| Morpho-logical characters     | <i>C. alpinus</i> Lectotype | Both lakes           |             |              | Lake Thun     |            |                | Lake Brienz  |               |             |              |            |               |              |               |             |  |
|-------------------------------|-----------------------------|----------------------|-------------|--------------|---------------|------------|----------------|--------------|---------------|-------------|--------------|------------|---------------|--------------|---------------|-------------|--|
|                               |                             | Non-types both sexes |             |              | Non-types     |            |                | Non-types    |               |             |              |            |               |              |               |             |  |
|                               |                             | Mean ± StDev         | Range       | N-total = 30 | Mean ± StDev  | Range      | N-females = 12 | Mean ± StDev | Range         | N-total = 9 | Mean ± StDev | Range      | N-females = 6 | Mean ± StDev | Range         | N-males = 3 |  |
| SL (mm)                       | 283.0                       | 266.1±56.4           | (147-364)   | 288.3±45.1   | (210-364)     | 299.6±37.3 | (267-364)      | 273.3±52.2   | (210-352)     | 214.3±46.0  | (147-290)    | 240.1±27.9 | (213-290)     | 162.7±23.3   | (147-190)     |             |  |
| Percentage of standard length |                             |                      |             |              |               |            |                |              |               |             |              |            |               |              |               |             |  |
| PelVFB                        | 4.5                         | 4.2±0.4              | (3.1-5.0)   | 4.4±0.3      | (3.8-5.0)     | 4.3±0.4    | (3.8-5.0)      | 4.4±0.3      | (4.0-4.8)     | 3.7±0.3     | (3.1-4.4)    | 3.9±0.1    | (3.7-4.0)     | 3.5±0.5      | (3.1-4.0)     |             |  |
| PelVFS                        | 4.7                         | 6.1±0.8              | (4.7-7.6)   | 5.9±0.7      | (4.7-7.2)     | 5.9±0.7    | (4.8-6.6)      | 5.9±0.8      | (4.7-7.2)     | 6.7±0.5     | (5.9-7.6)    | 6.8±0.5    | (6.0-7.6)     | 6.5±0.6      | (5.9-7.1)     |             |  |
| PelVF                         | 18.1                        | 16.7±1.1             | (14.18-22)  | 16.6±0.9     | (14.7-18.2)   | 16.2±0.9   | (14.7-17.3)    | 17.2±0.6     | (16.3-18.2)   | 16.9±1.5    | (14.18-1)    | 16.9±1.6   | (14.18-1)     | 1.8±1.4      | (15.2-18)     |             |  |
| PelFB                         | 3.7                         | 3.3±0.3              | (2.5-3.7)   | 3.4±0.3      | (2.8-3.7)     | 3.4±0.3    | (3.4±0.3)      | 3.3±0.2      | (3.0-3.5)     | 3.0±0.3     | (2.5-3.5)    | 3.0±0.3    | (2.5-3.5)     | 3.1±0.3      | (2.8-3.3)     |             |  |
| PecF1                         | 18.7                        | 16.2±1.2             | (13.6-18.7) | 16.2±1.3     | (13.6-18.7)   | 16.0±1.4   | (13.6-18.6)    | 16.5±1.1     | (15.1-18.7)   | 16.3±1.1    | (13.9-17.1)  | 16.4±1.3   | (13.9-17.1)   | 16.1±0.9     | (15.1-16.8)   |             |  |
| PecF2                         | 19.7                        | 17±1.1               | (14.4-19.7) | 17±1.1       | (15.3-19.7)   | 16.8±1.1   | (15.3-19.1)    | 17.3±1.1     | (15.8-19.7)   | 16.9±1.2    | (14.4-17.7)  | 17±1.3     | (14.4-17.7)   | 16.7±1.1     | (15.5-17.6)   |             |  |
| DFB                           | 12.9                        | 12.8±0.9             | (10.7-14.7) | 12.9±0.9     | (11.5-14.7)   | 12.9±0.9   | (11.7-14.4)    | 12.9±0.9     | (11.5-14.7)   | 12.6±1.1    | (10.7-14.0)  | 12.6±1.1   | (10.7-14.0)   | 12.7±1.4     | (11.7-14.3)   |             |  |
| DFaE                          | na                          | 19.7±1.2             | (16.4-23.0) | 19.5±0.8     | (17.6-20.6)   | 19.3±0.8   | (17.6-20.5)    | 19.7±0.5     | (18.6-20.6)   | 20.3±1.8    | (16.4-23.0)  | 20.1±1.9   | (16.4-21.5)   | 20.9±1.9     | (19.5-23.0)   |             |  |
| DFAd                          | 22.6                        | 20.8±1.4             | (17.0-24.0) | 20.6±0.9     | (18.6-22.5)   | 20.4±0.8   | (18.6-21.3)    | 20.9±1.1     | (19.6-22.5)   | 21.4±2.0    | (17.0-24.0)  | 21.2±2.2   | (17.0-22.7)   | 21.7±2.0     | (20.0-24.0)   |             |  |
| DFFe                          | 5.6                         | 5.0±0.6              | (4.0-6.5)   | 4.8±0.5      | (4-5.8)       | 4.8±0.6    | (4.0-5.8)      | 4.9±0.4      | (4.2-5.5)     | 5.3±0.7     | (4.3-6.5)    | 5.2±0.6    | (4.3-5.9)     | 5.5±1.1      | (4.4-6.5)     |             |  |
| AFB                           | 12.5                        | 12.4±0.9             | (9.8-14.2)  | 12.5±0.9     | (10.3-14.2)   | 12.3±0.9   | (10.3-14.0)    | 12.8±0.8     | (11.1-14.2)   | 12.1±1.0    | (9.8-13.3)   | 12.1±1.1   | (9.8-12.9)    | 12.2±1.0     | (11.4-13.3)   |             |  |
| AFaE                          | 14                          | 12.3±0.9             | (9.8-13.8)  | 12.2±0.7     | (10.5-13.3)   | 11.9±0.7   | (10.5-12.7)    | 12.5±0.7     | (10.9-13.3)   | 12.5±1.3    | (9.8-13.8)   | 12.6±1.4   | (9.8-13.8)    | 12.4±1.3     | (11.2-13.7)   |             |  |
| ADFB                          | 4.8                         | 4.4±0.6              | (3.4-5.5)   | 4.3±0.6      | (3.4-5.5)     | 4.3±0.6    | (3.5-5.5)      | 4.2±0.5      | (3.4-4.7)     | 4.7±0.5     | (3.8-5.4)    | 4.6±0.5    | (3.8-5.1)     | 4.9±0.5      | (4.5-5.4)     |             |  |
| CF                            | na                          | 24±1.4               | (19.1-26.3) | 24±1         | (21.9-26)     | 23.8±0.7   | (22.7-24.8)    | 24.3±1.2     | (21.9-26)     | 24.1±2.2    | (19.1-26.3)  | 24±2.6     | (19.1-26.3)   | 24.3±1.5     | (22.9-25.9)   |             |  |
| CD                            | 8.8                         | 8.1±0.5              | (6.7-8.9)   | 8.2±0.4      | (7.6-8.9)     | 8.1±0.3    | (7.6-8.6)      | 8.3±0.4      | (7.8-8.9)     | 7.8±0.6     | (6.7-8.6)    | 7.8±0.6    | (6.7-8.6)     | 7.8±0.8      | (7-8.4)       |             |  |
| CL                            | 12.6                        | 12.6±0.8             | (11.2-14.4) | 12.6±0.9     | (11.2-14.4)   | 12.5±0.8   | (11.2-13.6)    | 12.9±0.9     | (11.8-14.4)   | 12.5±0.9    | (11.3-13.9)  | 12.5±0.8   | (11.3-13.6)   | 12.5±1.2     | (11.5-13.9)   |             |  |
| PaDc                          | 18.4                        | 17.7±1.1             | (15.3-19.5) | 17.8±1       | (15.7-19.4)   | 17.8±1     | (16.2-19.4)    | 17.8±1       | (16.2-19.4)   | 17.6±1.3    | (15.3-19.5)  | 17.3±1.4   | (15.3-19.5)   | 18.3±1.1     | (17.2-19.3)   |             |  |
| DHL                           | 15.3                        | 14.6±0.9             | (12.6-16.3) | 14.2±0.6     | (12.6-15.6)   | 14.1±0.8   | (12.6-15.6)    | 14.3±0.5     | (13.7-15.0)   | 15.4±0.8    | (14.0-16.3)  | 15.2±0.9   | (14.0-16.3)   | 15.8±0.2     | (15.6-16.0)   |             |  |
| PreP                          | 53.6                        | 51.5±2.3             | (42.7-55.2) | 51.9±1.8     | (48-55.2)     | 51.8±1.8   | (49.3-55.2)    | 52.1±1.9     | (48.0-54.5)   | 50.3±3.1    | (42.7-53.0)  | 50.1±3.8   | (42.7-53.0)   | 51.4±0.7     | (50.6-51.9)   |             |  |
| PreA                          | 77.2                        | 78.3±1.5             | (75.2-81.8) | 78.5±1.4     | (75.2-81.1)   | 78.8±1.3   | (76.5-81.1)    | 78.1±1.5     | (75.2-80.3)   | 77.8±1.8    | (76.1-81.8)  | 78.2±2.0   | (76.1-81.8)   | 76.8±0.3     | (76.5-77.0)   |             |  |
| PreD                          | 45                          | 47.8±2               | (39.9-50.3) | 48±1.5       | (45.5-50.3)   | 48.3±1.5   | (45.5-50.3)    | 47.6±1.7     | (45.6-50)     | 47.3±3      | (39.9-50.2)  | 47.1±3.6   | (39.9-50.2)   | 47.8±1.6     | (46.3-49.5)   |             |  |
| BD                            | 27.6                        | 26.5±2.7             | (19.9-31.8) | 27.5±1.9     | (24.5-31.8)   | 28.2±2.0   | (25.2-31.8)    | 26.5±1.4     | (24.5-28.8)   | 24.2±2.9    | (19.9-27.0)  | 24.8±2.8   | (19.9-27.0)   | 23.1±3.3     | (20.5-26.8)   |             |  |
| PostD                         | 43.7                        | 42.6±2               | (34.7-46)   | 42.7±1.3     | (38.3-43.9)   | 42.3±1.5   | (38.3-43.9)    | 43.2±0.5     | (42.1-43.8)   | 42.3±3.3    | (34.7-46)    | 42.3±4.1   | (34.7-46)     | 42.5±0.9     | (41.4-43)     |             |  |
| TL                            | 118                         | 120.5±4.2            | (100-124.2) | 121±1.3      | (118.7-123.4) | 120.6±1.5  | (118.7-123.4)  | 121.5±0.7    | (120.8-122.8) | 119.2±7.5   | (100-124.2)  | 118.6±9.3  | (100-124.2)   | 120.5±1.7    | (118.9-122.4) |             |  |
| HL (mm)                       | 58.6                        | 54.2±10.6            | (31.1-73.1) | 58.3±8.6     | (41.9-73.1)   | 60.2±6.8   | (53-73.1)      | 55.7±10.4    | (41.9-72.2)   | 44.6±8.7    | (31.1-58.3)  | 49.5±4.7   | (45.7-58.3)   | 34.9±6       | (31.1-41.8)   |             |  |
| Percentage of head length     |                             |                      |             |              |               |            |                |              |               |             |              |            |               |              |               |             |  |
| SN                            | 22.2                        | 23.1±1.6             | (20.1-26.4) | 23.5±1.5     | (20.9-26.4)   | 23.7±1.5   | (21.4-26.4)    | 23.2±1.5     | (20.9-25.3)   | 22.4±1.6    | (20.1-25)    | 22.8±1.7   | (20.3-25)     | 21.7±1.4     | (20.1-22.7)   |             |  |
| ED                            | 22.1                        | 22.5±2               | (19.5-27.2) | 21.7±1.5     | (19.5-26.1)   | 21.3±1.1   | (19.5-22.9)    | 22.3±2       | (19.8-26.1)   | 24.3±1.7    | (21.8-27.2)  | 23.3±1.1   | (21.8-24.9)   | 26.1±1       | (25.4-27.2)   |             |  |
| EC                            | 28.9                        | 27.4±1.7             | (24.5-31.5) | 26.7±1.2     | (24.5-29)     | 26.6±1     | (24.9-28.3)    | 26.9±1.4     | (24.5-29)     | 29±1.9      | (26.4-31.5)  | 28.1±1.7   | (26.4-30.6)   | 30.6±0.8     | (29.9-31.5)   |             |  |

| Morpho-logical characters | <i>C. alpinus</i><br>Lectotype | Both lakes           |              | Lake Thun            |              |                        |              | Lake Brienz         |              |                     |              |                       |              |                     |             |
|---------------------------|--------------------------------|----------------------|--------------|----------------------|--------------|------------------------|--------------|---------------------|--------------|---------------------|--------------|-----------------------|--------------|---------------------|-------------|
|                           |                                | Non-types both sexes |              | Non-types            |              | Non-types              |              | Non-types           |              | Non-types           |              | Non-types             |              |                     |             |
|                           |                                | <i>N</i> -total = 30 |              | <i>N</i> -total = 21 |              | <i>N</i> -females = 12 |              | <i>N</i> -males = 9 |              | <i>N</i> -total = 9 |              | <i>N</i> -females = 6 |              | <i>N</i> -males = 3 |             |
|                           | Mean ± StDev                   | Range                | Mean ± StDev | Range                | Mean ± StDev | Range                  | Mean ± StDev | Range               | Mean ± StDev | Range               | Mean ± StDev | Range                 | Mean ± StDev | Range               |             |
| EH                        | 23.7                           | 22.2 ± 1.8           | (19.1-27.1)  | 21.4 ± 1.4           | (19.1-23.6)  | 21.1 ± 1.2             | (19.1-23.3)  | 21.9 ± 1.6          | (19.6-23.6)  | 23.9 ± 1.5          | (22.4-27.1)  | 23.3 ± 0.9            | (22.4-24.6)  | 25.1 ± 2            | (23.2-27.1) |
| ES                        | 5.7                            | 5.0 ± 0.8            | (3.3-6.3)    | 5.1 ± 0.8            | (3.4-6.3)    | 5.0 ± 0.7              | (3.4-6.0)    | 5.2 ± 0.9           | (3.4-6.3)    | 4.7 ± 0.8           | (3.3-5.8)    | 4.6 ± 0.9             | (3.3-5.5)    | 4.9 ± 0.8           | (4.3-5.8)   |
| PostO                     | 51.2                           | 52.4 ± 1.5           | (48.9-55.4)  | 52.6 ± 1.2           | (50.2-55.4)  | 52.5 ± 1.3             | (50.2-57.6)  | 52.8 ± 1.2          | (50.2-54.4)  | 51.7 ± 1.9          | (48.9-54.8)  | 52.2 ± 1.5            | (50.7-54.8)  | 50.8 ± 2.6          | (48.9-53.8) |
| HD                        | 71.7                           | 71 ± 3.7             | (65.5-79.6)  | 71.6 ± 4             | (65.6-79.6)  | 71.5 ± 4.6             | (65.6-79.6)  | 71.8 ± 3.4          | (67.9-76.7)  | 69.4 ± 2.5          | (65.5-73.2)  | 69.7 ± 2.7            | (65.5-73.2)  | 68.7 ± 2.3          | (66.3-70.8) |
| MW                        | 8.9                            | 9.4 ± 0.5            | (8.4-10.4)   | 9.4 ± 0.5            | (8.4-10.4)   | 9.3 ± 0.6              | (8.4-10.4)   | 9.4 ± 0.6           | (8.4-10.2)   | 9.5 ± 0.5           | (8.7-10.2)   | 9.6 ± 0.5             | (9.2-10.2)   | 9.3 ± 0.5           | (8.7-9.7)   |
| UJ                        | 27.8                           | 27.4 ± 1.5           | (24.3-30.1)  | 27.7 ± 1.5           | (24.3-29.4)  | 27.2 ± 1.5             | (24.3-29.4)  | 28.4 ± 1.3          | (26.5-30.1)  | 26.8 ± 1.3          | (25.4-29.1)  | 26.5 ± 1              | (25.6-28.2)  | 27.3 ± 1.8          | (25.4-29.1) |
| LJ                        | 38.2                           | 38.4 ± 1.7           | (36.6-41.4)  | 38.6 ± 1.7           | (36.6-41.4)  | 38.5 ± 1.8             | (36.6-41.4)  | 38.7 ± 1.6          | (37.4-1.2)   | 38.2 ± 1.8          | (33.8-39.4)  | 38 ± 2.1              | (33.8-39.2)  | 38.5 ± 1.3          | (36.9-39.4) |
| M                         | 22.5                           | 20 ± 1.2             | (16.6-22.5)  | 20 ± 1.1             | (17.7-22.1)  | 19.7 ± 0.9             | (18.4-21)    | 20.3 ± 1.3          | (17.7-22.1)  | 20 ± 1.6            | (16.6-22.5)  | 19.6 ± 1.6            | (16.6-21.1)  | 20.8 ± 1.5          | (19.5-22.5) |
| SD                        | 9.9                            | 10.1 ± 1.4           | (7.2-12.9)   | 10.5 ± 1.3           | (8.5-12.9)   | 10.5 ± 1.4             | (8.5-12.9)   | 10.6 ± 1.2          | (8.7-12.2)   | 9.2 ± 1.1           | (7.2-10.5)   | 9.2 ± 0.8             | (7.9-10)     | 9.3 ± 1.9           | (7.2-10.5)  |
| SW                        | 13.8                           | 15.6 ± 1.1           | (13.7-17.6)  | 15.6 ± 1.2           | (13.7-17.6)  | 15.7 ± 1.1             | (14.1-17.6)  | 15.5 ± 1.4          | (13.7-17.2)  | 15.7 ± 0.9          | (14.6-17.6)  | 15.6 ± 0.8            | (14.6-16.7)  | 16 ± 1.3            | (15.3-17.6) |
| HW                        | 47.1                           | 50 ± 4.5             | (39.2-59.5)  | 51.3 ± 4.1           | (44.2-59.5)  | 51.5 ± 5               | (44.2-59.5)  | 51 ± 2.8            | (46.3-55.9)  | 46.9 ± 4            | (39.2-52.3)  | 47.4 ± 5              | (39.2-52.3)  | 45.8 ± 0.4          | (45.4-46.1) |
| IOW                       | 24.5                           | 27.7 ± 2.2           | (22.4-32.5)  | 28.3 ± 2.3           | (22.4-32.5)  | 28 ± 2.4               | (22.4-32.4)  | 28.7 ± 2.3          | (24.9-32.5)  | 26.5 ± 1.2          | (24.9-28)    | 26.5 ± 1.4            | (24.9-28)    | 26.6 ± 1            | (25.5-27.4) |
| INW                       | 10.7                           | 11.7 ± 1             | (9.5-14.1)   | 12.1 ± 1             | (10.5-14.1)  | 12 ± 1.1               | (10.5-14.1)  | 12.1 ± 0.9          | (10.7-14)    | 11 ± 0.7            | (9.5-11.9)   | 10.9 ± 0.9            | (9.5-11.9)   | 11.2 ± 0.4          | (10.9-11.6) |
| LjW                       | 10.3                           | 11.1 ± 2.2           | (7.3-15.7)   | 12.1 ± 1.7           | (10.1-15.7)  | 11.9 ± 1.8             | (10.1-15.4)  | 12.4 ± 1.6          | (10.5-15.7)  | 8.8 ± 1.2           | (7.3-10.6)   | 9 ± 1.2               | (7.5-10.6)   | 8.5 ± 1.4           | (7.3-10.1)  |
| UjW                       | 19.8                           | 23.2 ± 2.2           | (18.4-27.2)  | 23.5 ± 2.2           | (19.9-27.2)  | 23 ± 2.5               | (19.9-27.2)  | 24.1 ± 1.6          | (21.9-26.5)  | 22.8 ± 2.2          | (18.4-25.6)  | 23.7 ± 1.6            | (21.4-25.6)  | 20.9 ± 2.2          | (18.4-22.8) |
| MGR                       | 10.6                           | 10.9 ± 1.4           | (8.3-15.2)   | 11.3 ± 1.4           | (9.3-15.2)   | 11.3 ± 1.4             | (9.3-15.2)   | 11.3 ± 1.4          | (9.5-13.2)   | 9.8 ± 1             | (8.3-11.2)   | 9.9 ± 1.1             | (8.3-11.2)   | 9.7 ± 0.8           | (8.7-10.2)  |
| LGR                       | 11.5                           | 11.9 ± 1.2           | (10.1-15.2)  | 12.3 ± 1.1           | (10.6-15.2)  | 12.2 ± 1.2             | (10.6-15.2)  | 12.5 ± 1            | (11.3-14.1)  | 10.8 ± 0.7          | (10.1-12.3)  | 10.9 ± 0.8            | (10.1-12.3)  | 10.6 ± 0.6          | (10.1-11.2) |
| UA                        | na                             | 18.5 ± 1.4           | (15.6-21.5)  | 18.4 ± 1.3           | (15.6-20.7)  | 18.6 ± 1.5             | (15.6-20.7)  | 18.2 ± 1.1          | (16.1-19.7)  | 18.7 ± 1.7          | (16.4-21.5)  | 18.2 ± 1.4            | (16.4-20)    | 19.8 ± 1.7          | (18.2-1.5)  |
| LA                        | 35                             | 33.9 ± 2.1           | (28.6-38.8)  | 33.5 ± 1.8           | (28.6-36.3)  | 34.1 ± 1.5             | (30.9-36.3)  | 32.7 ± 1.9          | (28.6-35)    | 34.7 ± 2.7          | (30.4-38.8)  | 34.5 ± 2.7            | (30.4-38.2)  | 35.1 ± 3.2          | (32.8-38.8) |
| Meristic characters       |                                | Mode                 | Range        | Mode                 | Range        | Mode                   | Range        | Mode                | Range        | Mode                | Range        | Mode                  | Range        | Mode                | Range       |
| PelvF unbranched          | 1                              | 1                    | (1-1)        | 1                    | (1-1)        | 1                      | (1-1)        | 1                   | (1-1)        | 1                   | (1-1)        | 1                     | (1-1)        | 1                   | (1-1)       |
| PelvF branched            | 11                             | 11                   | (10-11)      | 11                   | (10-11)      | 11                     | (10-11)      | 11                  | (10-11)      | 10                  | (10-11)      | 10                    | (10-11)      | 11                  | (10-11)     |
| PecF unbranched           | 1                              | 1                    | (1-1)        | 1                    | (1-1)        | 1                      | (1-1)        | 1                   | (1-1)        | 1                   | (1-1)        | 1                     | (1-1)        | 1                   | (1-1)       |
| PecF branched             | 16                             | 15                   | (14-17)      | 15                   | (14-17)      | 15                     | (14-17)      | 16                  | (14-16)      | 15                  | (15-17)      | 15                    | (15-16)      | na                  | (15-17)     |
| DF unbranched             | 3                              | 4                    | (3-4)        | 4                    | (3-4)        | 4                      | (3-4)        | 4                   | (3-4)        | 4                   | (3-4)        | 4                     | (3-4)        | 4                   | (4-4)       |
| DF branched               | 11                             | 11                   | (10-13)      | 11                   | (10-13)      | 11                     | (10-13)      | 11                  | (10-12)      | 11                  | (10-11)      | 11                    | (10-11)      | 11                  | (11-11)     |
| AF unbranched             | 3                              | 3                    | (3-4)        | 3                    | (3-4)        | 3                      | (3-3)        | 3                   | (3-4)        | 4                   | (3-4)        | 4                     | (3-4)        | 4                   | (3-4)       |

| Meristic characters | <i>C. alpinus</i><br>Lectotype | Both lakes           |      |         | Lake Thun           |         |       |                       |      |       | Lake Brienz        |      |       |                    |      |       |                      |      |       |                    |      |       |         |  |
|---------------------|--------------------------------|----------------------|------|---------|---------------------|---------|-------|-----------------------|------|-------|--------------------|------|-------|--------------------|------|-------|----------------------|------|-------|--------------------|------|-------|---------|--|
|                     |                                | Non-types both sexes |      |         | Non-types           |         |       | Non-types             |      |       | Non-types          |      |       | Non-types          |      |       | Non-types            |      |       |                    |      |       |         |  |
|                     |                                | <i>N-total</i> = 30  |      |         | <i>N-total</i> = 21 |         |       | <i>N-females</i> = 12 |      |       | <i>N-males</i> = 9 |      |       | <i>N-total</i> = 9 |      |       | <i>N-females</i> = 6 |      |       | <i>N-males</i> = 3 |      |       |         |  |
| Mode                | Range                          |                      | Mode | Range   |                     | Mode    | Range |                       | Mode | Range |                    | Mode | Range |                    | Mode | Range |                      | Mode | Range |                    | Mode | Range |         |  |
| AF branched         | 12                             | (10-14)              |      | 12      | (10-14)             |         | 12    | (10-14)               |      | 12    | (10-13)            |      | 11    | (11-13)            |      | 12    | (11-13)              |      | 11    | (11-13)            |      | 11    | (11-11) |  |
| LS                  | 82                             | (77-93)              | 81   | (77-93) | 84                  | (77-93) | 80    | (78-84)               |      | 84    | (80-88)            |      | 84    | (80-88)            |      | 86    | (80-88)              |      | na    | (81-84)            |      | na    | (81-84) |  |
| PDS                 | 39                             | (32-42)              | 36   | (32-42) | 36                  | (32-42) | 33    | (33-38)               |      | 33    | (33-38)            |      | 33    | (32-42)            |      | na    | (33-42)              |      | na    | (32-37)            |      | na    | (32-37) |  |
| TDS                 | 10                             | (8-11)               | 10   | (9-11)  | 10                  | (9-11)  | 10    | (9-11)                |      | 10    | (9-11)             |      | 10    | (8-10)             |      | 10    | (8-10)               |      | 9     | (9-10)             |      | 9     | (9-10)  |  |
| TAS                 | 8                              | (7-9)                | 8    | (8-9)   | 8                   | (8-9)   | 8     | (8-9)                 |      | 8     | (8-9)              |      | 8     | (7-8)              |      | 8     | (7-8)                |      | 8     | (7-8)              |      | 8     | (7-8)   |  |
| TPS                 | 8                              | (7-9)                | 9    | (8-9)   | 9                   | (8-9)   | 8     | (8-9)                 |      | 8     | (8-9)              |      | 8     | (7-8)              |      | 8     | (8-8)                |      | 8     | (7-8)              |      | 8     | (7-8)   |  |
| UGR                 | 10                             | (8-11)               | 10   | (8-11)  | 10                  | (9-11)  | 11    | (8-11)                |      | 11    | (8-11)             |      | 9     | (9-11)             |      | 9     | (9-11)               |      | na    | (9-11)             |      | na    | (9-11)  |  |
| LGR                 | 18                             | (15-23)              | 19   | (16-23) | 19                  | (16-21) | 20    | (17-23)               |      | 18    | (17-23)            |      | 18    | (15-21)            |      | 17    | (17-21)              |      | na    | (15-19)            |      | na    | (15-19) |  |
| total GR            | 28                             | (25-34)              | 30   | (25-34) | 28                  | (26-32) | 30    | (25-34)               |      | 28    | (26-32)            |      | 28    | (26-30)            |      | 29    | (27-30)              |      | 28    | (26-28)            |      | 28    | (26-28) |  |

HL, mean = 42.2), a narrower snout (14.6–17.6% HL, mean = 15.7 vs. 15.7–20.2% HL, mean = 17.8), a narrower lower jaw (7.3–10.6% HL, mean = 8.8 vs. 10.1–14.1% HL, mean = 11.5) and shorter gill rakers (middle gill raker length: 8.3–11.2% HL, mean = 9.8 vs. 10.9–15.1% HL, mean = 13.5; longest gill raker length: 10–12.3% HL, mean = 10.8 vs. 12.1–16.8% HL, mean = 14.7). For fish larger than 163.5 mm SL, *C. alpinus* from Lake Brienz can be distinguished based on ratios from *C. brienzi* by having a larger “caudal peduncle depth / snout width” ratio (CD/SW: 2.25–2.64 vs. 1.82–2.04), “length of the erected anterior part of the dorsal fin / length from the adipose fin to the caudal fin base” ratio (DFAe/PAdC: 1.11–1.32 vs. 0.96–1.16) and by having a smaller “lower jaw width / upper jaw width” ratio (LJW/UJW: 0.33–0.44 vs. 0.45–0.55). With the full size range (100–290 mm) of Lake Brienz specimens, *C. alpinus* can be distinguished from *C. brienzi* by having a larger “length of the depressed anterior part of the dorsal fin / lower jaw width” ratio (DFAd/LJW: 9.84–14.82 vs. 6.05–8.91), “dorsal head length / lower jaw length” ratio (DHL/LJ: 1.84–2.22 vs. 1.63–1.82), “head depth / lower jaw width” ratio (HD/LJW: 6.72–9.39 vs. 5.23–6.66), “head length / lower jaw length” ratio (HL/LJ: 2.54–2.96 vs. 2.19–2.47) and a smaller “length of the pectoral fin 2 / length of the depressed anterior part of the dorsal fin” ratio (PecF2/DFAd: 0.74–0.85 vs. 0.85–1.03) (Tables 4, 7, 11).

#### ***Coregonus alpinus*-*Coregonus profundus***

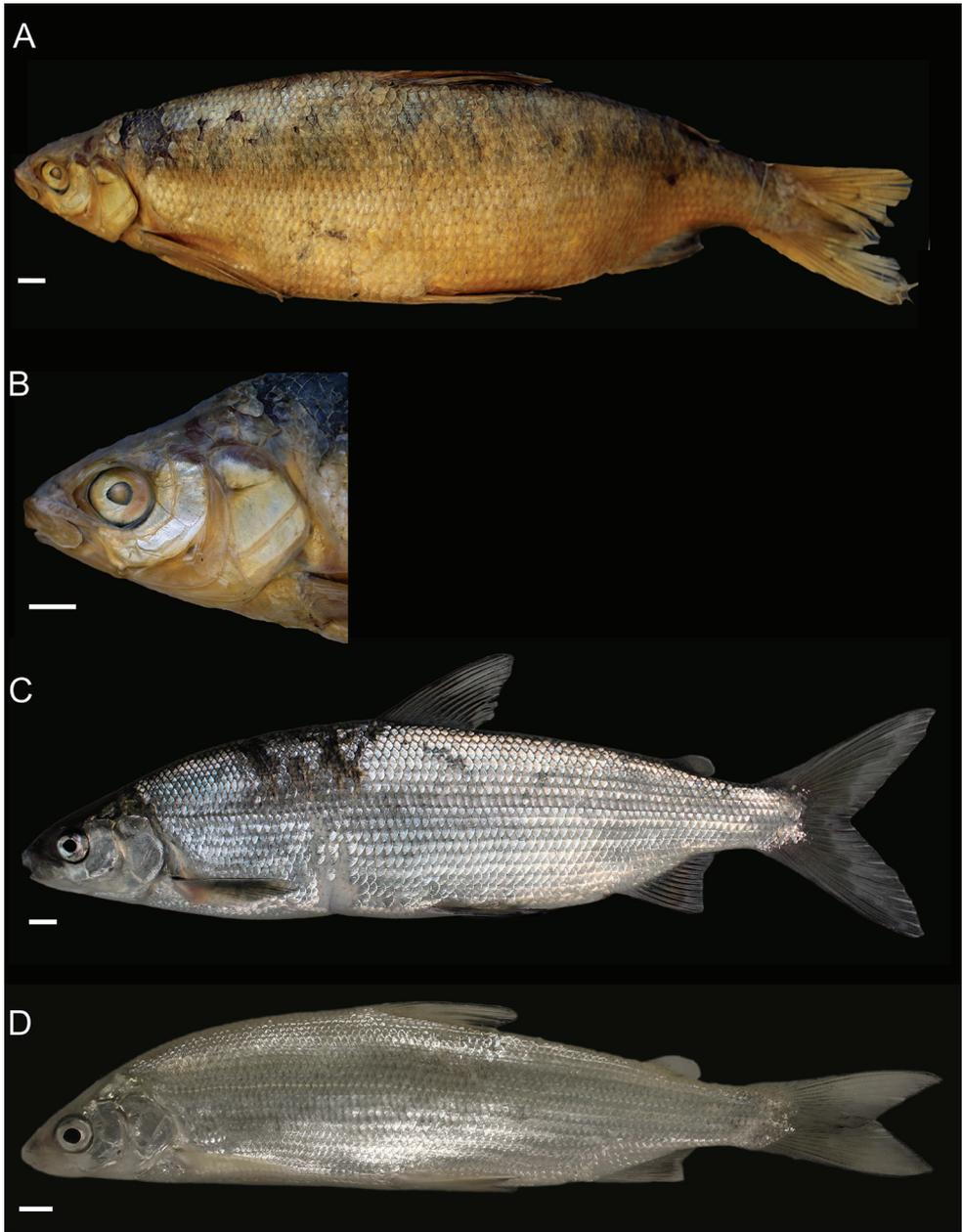
*Coregonus alpinus* from Thun differs from *C. profundus* by having shorter pectoral fins (pectoral fin 1 length: 13.6–18.7% SL, mean = 16.2 vs. 16.6–21% SL, mean = 18.4; pectoral fin 2 length: 15.3–19.7% HL, mean = 17 vs. 17.7–23.2% SL, mean = 20.2), a deeper caudal peduncle (7.6–8.9% SL, mean = 8.2 vs. 6.5–7.9% SL, mean = 7.3), a shorter head (12.6–15.6% SL, mean = 14.2 vs. 15.5–18.4% SL, mean = 16.4) and longer gill rakers (middle gill raker length: 9.3–15.2% HL, mean = 11.3 vs. 7.6–11.7% HL, mean = 9.2; longest gill raker length: 10.6–15.2% HL, mean = 12.3 vs. 7.8–12.4% HL, mean = 10.1). Based on ratios *C. alpinus* can be distinguished from *C. profundus* by having a larger “caudal peduncle depth / dorsal head length” ratio (CD/DHL: 0.54–0.62 vs. 0.4–0.49) (Tables 4, 8, 10).

#### ***Coregonus alpinus*-*Coregonus acrinus***

*Coregonus alpinus* can further be differentiated from *C. acrinus* by having a shorter lower jaw (36.6–41.4% HL, mean = 38.6 vs. 38.6–47% HL, mean = 40.9). Based on ratios *C. alpinus* can be distinguished from *C. acrinus* by having a larger “caudal fin length / maxilla length” ratio (CF/M: 5.55–6.55 vs. 4.4–5.57) (Tables 4, 9, 10).

**Description.** General appearance is shown in Figure 5. Morphological and meristic characters of both sexes can be found in Table 4 and Suppl. material 1: Table S6 and first- and second-best ratios for both sexes combined can be found in Tables 10, 11. The description is valid for both sexes and both lakes; differences between the populations of lakes Thun and Brienz are mentioned.

**Shape:** Generally deep bodied with greatest body depth anterior of the dorsal fin. Dorsal profile strongly arched compared to ventral profile such that the dorsal profile from the tip of snout to the anterior origin of dorsal fin is moderate to strongly convex. Ventral profile slightly arched such that almost straight or slightly convex from the



**Figure 5.** *Coregonus alpinus*, lakes Thun and Brienz, Switzerland **A** lectotype, MHNG-717.045, Lake Thun, 283 mm SL, sex unknown **B** close-up of head of lectotype MHNG-717.045 **C** non-type, NMBE-1077246, Lake Thun, 251.5 mm SL, male, freshly caught specimen **D** non-type, NMBE-1077115, Lake Brienz, 253 mm SL, female, frozen and defrosted specimen. The white scale (1cm) below each fish acts as a reference for the actual size of the specimen.

interorbital area to the pelvic fin origin. Head short. Mouth thin (i.e., width of upper and lower jaw), short and sub-terminal. Rostral plate pronounced and almost equally wide as deep resulting in an almost square shape. Tip of the snout often blunt. Small eye, which is less pronounced in specimens from Lake Brienz. Eye-socket thick and triangular (i.e., sickle-shaped). Pectoral fin moderately tapered. Dorsal fin long with the anterior unbranched ray of the erected dorsal fin approx. 60–70° angle to body axis and only slightly bent posteriorly at the end of the ray. Caudal peduncle stout and short with the caudal fin forked and sometimes lightly asymmetrical with either the ventral or dorsal part being longer. Unbranched ray of anal fin slightly bent posteriorly. Anal fin longest anteriorly and progressively shortening posteriorly with the outer margin of the anal fin mostly straight and only rarely slightly concave.

**Meristics:** Few short gill rakers, which are shorter for specimens from Lake Brienz.

**Colour:** Pigmentation of fins and body over all strong in live specimens. In specimens from Lake Thun the pectoral fin is moderately to strongly pigmented. Dorsal, adipose, pelvic, anal and caudal fins are strongly pigmented. In specimens from Lake Brienz all fins are less pigmented. The pectoral fin is sometimes yellowish and ranges from translucent to moderately pigmented at the median to distal parts of the fin. Dorsal, adipose, pelvic, anal, and caudal fins are moderately pigmented. In both lakes fish have a silvery appearance along the flanks with few to many pigmented small dots on the scales along the flank and the dorsum (as can be found for the species of *C. fatioidi*, *C. steinmanni*, *C. brienzii*). The distribution of the dots is bound to the scale patterning such that the dots are found at the edge of the scales or at the boundary point of two scales. Dorsally above the lateral line the silvery appearance changes to a light (e.g., RGB (135, 236, 179)) or darker greenish blue colour (e.g., RGB (7,168,125)). The dorsal part of the head of specimens of Lake Brienz is moderately pigmented, whereas that of specimens from Lake Thun is strongly pigmented. The snout around the nostrils is moderately (Lake Brienz) to strongly (Lake Thun) pigmented. Specimens in Lake Brienz have a gap of very weak pigmentation posteriorly of the nostrils up to the height of the middle of the eyes. The pre-operculum and operculum are silvery with one black dot on the lower margin of the pre-operculum. In some specimens of Lake Thun, the pre-operculum and operculum has some pigmented dots, similar to those found on the scales and extending also to the dorsal part of the head. For a comparison to the main colouration found in the other species see Suppl. material 1: Figure S8. Preserved specimens are pale in colouration with similar pigmentation as described for live specimens. The silvery, translucent, not coloured or unpigmented parts of the body become brown-yellowish (e.g., RGB (239, 210, 40)), whereas the pigmented parts are conserved and the coloured parts (dorsally above the lateral line) become brownish (e.g., RGB (186, 140, 100)).

**Distribution and notes on biology.** *Coregonus alpinus* is found in the lakes Thun (46°40'N, 7°46'E) and Brienz (46°43'N, 7°57'E) that are connected through the river Aare at Interlaken. *Coregonus alpinus* feeds predominantly on benthic prey and parts

of the year on zooplankton (stomach content for Lake Brienz: Maurer and Guthruf 2005; Müller et al. 2007; isotopic signature for both lakes: Selz 2008; Hudson 2011; Ingram et al. 2012) and has a rapid growth rate (Lake Brienz: Müller et al. 2007; both lakes: Kirchhofer 1995; Bittner et al. unpublished). It has to be noted that the stomach content and isotopic work did not distinguish between all species in lakes Thun or Brienz and thus in some cases lumped different species together into few groups. The stomach content work by Maurer and Guthruf (2005) and Müller et al. (2007) differentiated between “small-type” and “large-type” whitefish based on cohort-specific threshold values for length-at-age. Based on morphology and ecology Kirchhofer (1995) differentiated in Lake Thun between “Albock” (comprising most likely of *C. alpinus*, *C. steinmanni* and *C. acrinasus*), “Brienzig” (comprising most likely of *C. albellus* and *C. fatioi*) and “Kropfer” (*C. profundus*) and in Lake Brienz between “Felchen” (comprising most likely of *C. alpinus*, *C. fatioi* and *C. brienzi*) and “Brienzig” and “Winter-Brienzig” (comprising of summer- and winter-spawning specimens of *C. albellus*). Finally, Selz (2008), Hudson (2011) and Ingram et al. (2012) did not yet differentiate between *C. alpinus* and *C. steinmanni* in Lake Thun, which were most likely both grouped under *C. “Balchen”*. The gill raker number and length of *C. alpinus* (few and short gill rakers) suggests, based on the functional properties of the number of gill rakers experimentally tested with specimens of this species and other whitefish species from lakes Thun and Lucerne (Lundsgaard-Hansen et al. 2013; Roesch et al. 2013), that *C. alpinus* feeds more on benthic prey and less on zooplankton. However, this assumption needs to be verified with stomach content analysis that distinguish between the different species within a lake. The relative species abundances in the pelagic and benthic habitat from a habitat-stratified random sampling of Lake Thun (mid-October 2013: Vonlanthen et al. 2015) and Brienz (mid-September 2011: Vonlanthen et al. 2013) shows, that *C. alpinus* can only be found in shallow water in the benthic habitat (first 15 m;  $N = 1$  each for lakes Thun and Brienz) and is completely absent from the pelagic habitat in Lake Thun, while in Lake Brienz it can be also found in the very shallow waters (approx. first 5 m;  $N = 2$ ) of the pelagic habitat (Dönz et al. 2018). It is noteworthy that the habitat-stratified random sampling data for both lakes only covers a short period of time (one month in late summer) and it is thus not clear how the species are distributed spatially throughout the rest of the year. In Lake Thun *C. alpinus* resembles phenotypically *C. steinmanni* and to some extent *C. acrinasus*. The average size (total length) at 3 years of age for specimens in this study is  $321 \pm 20$  mm (mean and standard deviation,  $N = 8$ ) and  $273 + 14$  mm ( $N = 4$ ) for lakes Thun and Brienz respectively (Suppl. material 1: Figures S4–S6). The average size at 3 years of age for the specimens of *C. alpinus* from Lake Thun from this study are similar to those for the years 1969–1970 ( $333.8 \pm$  mm,  $N = 13$ ) and 2004–2005 ( $342.8 \pm 21$  mm,  $N = 14$ ) (Bittner et al. unpublished; Vonlanthen et al. unpublished). In Lake Thun the size at 3 years of age of *C. alpinus* is similar to that of *C. steinmanni*, larger than that of *C. acrinasus* and considerably larger than that of *C. albellus*, *C. fatioi* and *C. profundus* (Suppl. material 1: Figure S6). In Lake Brienz the size at 3 years of age of *C. alpinus* is larger than that of *C. fatioi* and *C. brienzi* and

considerably larger than that of *C. albellus* (Suppl. material 1: Figure S6). However, the size-at-age comparisons should be treated with some caution since the sample size for *C. alpinus* is rather small. *Coregonus alpinus* has a short spawning season in late December and spawns mostly in very shallow water (1–2 m) and to a lesser extent down to 10 m and very seldom down to 30 m or more (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). *Coregonus alpinus* spawns earlier in Lake Brienz than in Lake Thun (Fatio 1890; Dönz et al. 2018). The spawning season and depth of *C. alpinus* overlaps largely with that of *C. acrinasus*, *C. fatioi* and *C. steinmanni* in Lake Thun and with that of *C. fatioi* and *C. brienzii* in Lake Brienz.

Kottelat (1997) has designated a lectotype as *C. alpinus* which is incongruent with his description of the species (with the common name "Kropfer": Kottelat (1997) and Kottelat and Freyhof (2007)). Fatio (1885, 1890) was unaware of this species (the "Kropfer") as it is not considered in his compendium of the Swiss fauna (Fatio 1890) nor in his earlier work on the Swiss whitefish (Fatio 1885). The lectotype designated by Kottelat (1997) to *C. alpinus* clearly and correctly resembles the description given by Fatio (Fatio 1885, 1890) for the species-group *Coregonus schinzii alpinus* (Fatio, 1885) and later *Coregonus schinzii helveticus* (Fatio, 1890), known then and today by its local name as "Balchen". Fatio (1890) describes the "Balchen"-type whitefish as a relatively large whitefish, with few and short gillrakers, a short and stout head with a thick and squared snout, mouth inferior and often subterminal especially for specimens from Lake Thun, a more or less small eye, caudal peduncle short and stout, long pectoral fin, all fins more or less strongly pigmented, colour of live specimens generally olive or grey-olive with greenish or blueish reflections on the back, head more or less strongly pigmented, black pigmented dots more or less abundant on the dorsum, and on the margins of the scales, spawning season in winter (November–December) and spawning depth rather shallow at the shoreline over boulders or stones (Fatio 1885: Page 663, Tables 1, 2; Fatio 1890: Pages 222–234). This description is very clearly and accurately that of a "Balchen", and very different from "Kropfer". We thus identify *C. alpinus* as the species from lakes Thun and Brienz known under the common name "Balchen". The description of *C. alpinus* in Kottelat (1997) and Kottelat and Freyhof (2007) and the photograph in Kottelat and Freyhof (2007) does not describe and depict "Balchen" but *C. profundus*, the species from Lake Thun known by the common name "Kropfer".

**Common name.** Balchen.

### *Coregonus fatioi*, Kottelat, 1997

#### Figure 6

*Coregonus* "Albock": Heuscher 1901

*Coregonus* "Albock", "BR11": Douglas et al. 1999, 2003; Douglas and Brunner 2002  
(see also synonymy of *C. acrinasus*)

*Coregonus* "Felchen": Kirchhofer 1990; Kirchhofer 1995 (see also synonymy of *C. alpinus* and *C. brienzii*)

**Table 5.** Morphological and meristic data of *C. fatioid* Kottelat, 1997 from lakes Thun and Brienz, MHNG-809.059 lectotype from Lake Thun; non-type material N = 30 from Lake Thun and N = 30 from Lake Brienz.

| Morphological characters             | Both lakes           |                       |                         | Lake Thun               |                       |                       | Lake Brienz           |                       |                       |                      |                      |                      |                      |                      |
|--------------------------------------|----------------------|-----------------------|-------------------------|-------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|
|                                      | Non-types both sexes |                       |                         | Non-types               |                       |                       | Non-types             |                       |                       |                      |                      |                      |                      |                      |
|                                      | <i>N</i> total = 60  | Range                 | <i>N</i> females = 30   | Mean ± StDev            | Range                 | <i>N</i> females = 17 | Mean ± StDev          | Range                 | <i>N</i> females = 12 | Mean ± StDev         | Range                | <i>N</i> males = 18  | Mean ± StDev         | Range                |
| SL (mm)                              | 154.5                | 207.5±35.2 (132–288)  | 230.2±21.2 (191–288)    | 3.9±0.8 (3.2–4.8)       | 3.3–4.4 (3.3–4.4)     | 4.0±0.4 (4.0±0.4)     | 3.7±0.4 (3.1–4.6)     | 3.7±0.3 (3.1–4.1)     | 3.7±0.3 (3.2–4.6)     | 177.3±31.6 (132–225) | 184.8±29.7 (141–244) | 195.9±29.7 (132–244) | 177.3±31.6 (132–225) | 177.3±31.6 (132–225) |
| <b>Percentage of standard length</b> |                      |                       |                         |                         |                       |                       |                       |                       |                       |                      |                      |                      |                      |                      |
| PelVFB                               | 3.6                  | 3.8±0.4 (3.1–4.8)     | 4.0±0.4 (3.2–4.8)       | 3.9±0.8 (3.3–4.4)       | 3.3–4.4 (3.3–4.4)     | 4.0±0.4 (4.0±0.4)     | 3.7±0.4 (3.1–4.6)     | 3.7±0.3 (3.1–4.1)     | 3.7±0.3 (3.2–4.6)     |                      |                      |                      |                      |                      |
| PelVFS                               | 5.4                  | 6.2±0.8 (3.9–8.0)     | 6.2±0.9 (3.9–8.0)       | 6.3±0.8 (4.6–7.4)       | 4.6–7.4 (4.6–7.4)     | 6.1±1.0 (6.1±1.0)     | 6.2±0.8 (3.9–7.4)     | 6.2±0.8 (3.9–7.0)     | 6.2±0.8 (3.9–7.4)     |                      |                      |                      |                      |                      |
| PelVF                                | 17.4                 | 16.1±1 (13.7–19.3)    | 16.4±1.2 (13.7–19.3)    | 16.6±1 (15.1–19.3)      | 16.1±1.4 (13.7–18.6)  | 16.1±1.4 (13.7–18.6)  | 15.8±0.8 (14.6–17.4)  | 15.8±0.7 (14.7–17.1)  | 15.9±0.8 (14.6–17.4)  |                      |                      |                      |                      |                      |
| PecVFB                               | 3.1                  | 3.2±0.3 (2.7–3.8)     | 3.3±0.3 (2.8–3.8)       | 3.2±0.3 (2.8–3.7)       | 3.4±0.3 (2.9–3.8)     | 3.4±0.3 (2.9–3.8)     | 3.1±0.2 (2.7–3.4)     | 3.0±0.2 (2.7–3.4)     | 3.1±0.2 (2.7–3.4)     |                      |                      |                      |                      |                      |
| PecF1                                | 17.8                 | 16.2±1.3 (13.3–18.9)  | 16.5±1.4 (13.3–18.9)    | 16.8±1.2 (14.7–18.9)    | 16.1±1.5 (13.3–18.4)  | 16.1±1.5 (13.3–18.4)  | 16.0±1.1 (14.1–18.7)  | 15.8±0.9 (14.2–17.3)  | 16.0±1.2 (14.1–18.7)  |                      |                      |                      |                      |                      |
| PecF2                                | 18.4                 | 17.2±1.4 (13.8–20.6)  | 17.7±1.5 (13.8–20.6)    | 18.1±1.4 (15.5–20.6)    | 17.2±1.7 (13.8–19.8)  | 17.2±1.7 (13.8–19.8)  | 16.8±1.1 (14.9–19.7)  | 16.5±0.9 (14.9–17.9)  | 17.1±1.2 (15.3–19.7)  |                      |                      |                      |                      |                      |
| DFB                                  | 11.4                 | 11.9±0.7 (10.3–13.3)  | 11.8±0.7 (10.3–13.1)    | 11.6±0.7 (10.3–13.1)    | 11.6±0.7 (10.3–12.9)  | 12.0±0.6 (11.2–13.1)  | 12.0±0.7 (10.3–13.3)  | 12.0±0.6 (11.3–12.6)  | 12.0±0.9 (10.3–13.3)  |                      |                      |                      |                      |                      |
| DFaE                                 | na                   | 17.9±1.3 (15.4–21.9)  | 18.0±1.4 (15.4–21.9)    | 18.4±1.4 (15.4–21.9)    | 17.4±1.2 (15.8–19.8)  | 17.4±1.2 (15.8–19.8)  | 17.8±1.1 (15.7–20.0)  | 17.6±1.0 (15.7–19.4)  | 18.0±1.2 (16.5–20.0)  |                      |                      |                      |                      |                      |
| DFAd                                 | 19.1                 | 19.1±1.3 (16.7–23.5)  | 19.3±1.4 (16.7–23.5)    | 19.7±1.4 (16.7–23.5)    | 18.8±1.3 (17.0–21.3)  | 18.8±1.3 (17.0–21.3)  | 18.8±1.1 (17.1–21.1)  | 18.8±0.9 (17.1–20.3)  | 18.8±1.3 (17.1–21.1)  |                      |                      |                      |                      |                      |
| DFPe                                 | 6.3                  | 5.1±0.6 (3.9–7.0)     | 5.0±0.7 (3.9–6.9)       | 5.1±0.7 (3.9–6.9)       | 4.8±0.7 (4.1–6.3)     | 4.8±0.7 (4.1–6.3)     | 5.3±0.5 (4.3–7.0)     | 5.3±0.5 (4.7–6.3)     | 5.3±0.6 (4.3–7.0)     |                      |                      |                      |                      |                      |
| AFB                                  | 12.1                 | 12.3±0.9 (10.6–15.1)  | 12.6±1.0 (10.7–15.1)    | 12.5±1.0 (10.7–14.0)    | 12.8±1.1 (11.7–15.1)  | 12.8±1.1 (11.7–15.1)  | 11.9±0.8 (10.6–13.3)  | 12.0±0.6 (11.4–13.0)  | 11.9±0.8 (10.6–13.3)  |                      |                      |                      |                      |                      |
| AFaE                                 | na                   | 11.5±0.9 (9.8–13.9)   | 11.9±0.9 (10.2–13.9)    | 12.1±0.9 (10.5–13.9)    | 11.7±1.0 (10.2–13.3)  | 11.7±1.0 (10.2–13.3)  | 11.1±0.6 (9.8–12.7)   | 11.0±0.5 (9.8–11.9)   | 11.1±0.7 (10.2–12.7)  |                      |                      |                      |                      |                      |
| AdFB                                 | 5.7                  | 5.5±0.8 (4.0–8.1)     | 5.6±0.7 (4.6–8.1)       | 5.7±0.7 (4.8–8.1)       | 5.4±0.6 (4.6–6.9)     | 5.4±0.6 (4.6–6.9)     | 5.5±0.8 (4.0–7.7)     | 5.5±0.7 (4.3–6.7)     | 5.5±0.9 (4.0–7.7)     |                      |                      |                      |                      |                      |
| CF                                   | na                   | 23.8±1.3 (19.6–27.2)  | 23.6±1.3 (19.6–26.6)    | 23.9±1.1 (22.1–26.4)    | 23.3±1.6 (19.6–26.6)  | 23.3±1.6 (19.6–26.6)  | 24.1±1.2 (22.4–27.2)  | 23.8±1.3 (22.4–27.2)  | 24.1±1.1 (22.7–26.4)  |                      |                      |                      |                      |                      |
| CD                                   | 7.7                  | 7.9±0.3 (6.7–8.5)     | 7.1±0.3 (6.7–8.5)       | 7.1±0.4 (6.7–8.5)       | 7.2±0.2 (6.9–7.7)     | 7.2±0.2 (6.9–7.7)     | 7.3±0.3 (6.8–8)       | 7.3±0.3 (6.8–7.8)     | 7.4±0.3 (6.9–8)       |                      |                      |                      |                      |                      |
| CL                                   | 13.9                 | 13.7±0.9 (11.5–16.1)  | 13.3±0.8 (11.5–14.7)    | 13.1±0.8 (11.5–14.7)    | 13.5±0.6 (12.6–14.6)  | 13.5±0.6 (12.6–14.6)  | 14.2±0.8 (13.1–16.1)  | 13.9±0.7 (13.1–15.5)  | 14.3±0.8 (13.2–16.1)  |                      |                      |                      |                      |                      |
| PLdC                                 | 19.1                 | 18.9±1 (16.8–22.2)    | 18.8±1 (16.8–22.2)      | 18.6±1.1 (16.8–22.2)    | 19.0±0.8 (17.8–20.4)  | 19.0±0.8 (17.8–20.4)  | 19.1±1 (16.9–20.4)    | 18.7±1.1 (16.9–20.8)  | 19.1±1 (17.2–20.8)    |                      |                      |                      |                      |                      |
| DHL                                  | 15.9                 | 15.2±0.8 (13.6–16.8)  | 14.8±0.7 (13.6–16.2)    | 14.9±0.6 (13.9–16.1)    | 14.6±0.9 (13.6–16.2)  | 14.6±0.9 (13.6–16.2)  | 15.7±0.7 (14.5–16.8)  | 15.4±0.8 (14.5–16.8)  | 15.8±0.6 (14.7–16.7)  |                      |                      |                      |                      |                      |
| PreP                                 | 52.1                 | 52.0±1.5 (47.5–55.5)  | 51.8±1.7 (47.5–55.1)    | 52.2±1.7 (47.5–55.1)    | 51.3±1.6 (48.5–53.8)  | 52.1±1.3 (48.8–55.5)  | 52.7±1.4 (51.3–55.5)  | 51.8±1.1 (48.8–53.9)  | 51.8±1.1 (48.8–53.9)  |                      |                      |                      |                      |                      |
| PreA                                 | 78.8                 | 77.0±1.3 (74.4–80.2)  | 76.9±1.5 (74.4–80.2)    | 77.4±1.6 (74.7–80.2)    | 76.3±1.1 (74.4–78.1)  | 77.1±1.0 (74.4–78.1)  | 77.1±1.0 (74.4–78.1)  | 77.4±0.9 (76.4–79.2)  | 76.8±1.0 (75.2–78.6)  |                      |                      |                      |                      |                      |
| PreD                                 | 48.4                 | 46.8±1.3 (41.5–49.1)  | 46.8±1.5 (41.5–49.1)    | 46.5±1.7 (41.5–48.8)    | 47.2±1.1 (44.8–49.1)  | 47.2±1.1 (44.8–49.1)  | 46.8±1.0 (43.4–49)    | 46.9±1.0 (43.4–49)    | 46.9±1.0 (45.9–48)    |                      |                      |                      |                      |                      |
| BD                                   | 24.9                 | 24.4±1.4 (22.1–28.1)  | 24.9±1.4 (22.7–28.1)    | 25.3±1.3 (23.2–28.1)    | 24.4±1.4 (22.7–28.1)  | 24.4±1.4 (22.7–28.1)  | 23.9±1.2 (22.1–26.2)  | 24.7±1.1 (22.4–26.2)  | 23.4±0.9 (22.1–24.9)  |                      |                      |                      |                      |                      |
| PostD                                | 45.4                 | 44.5±1.4 (41.6–50.7)  | 44.9±1.7 (41.6–50.7)    | 44.5±2 (41.6–50.7)      | 45.3±1.2 (43.4–47.1)  | 44.2±0.9 (42.5–45.6)  | 44.5±1.2 (42.5–45.6)  | 44.3±1.1 (42.5–45.6)  | 44.3±1.1 (42.5–45.8)  |                      |                      |                      |                      |                      |
| TL                                   | na                   | 121.1±1.8 (117.3–126) | 120.7±1.9 (117.3–124.2) | 121.3±1.7 (117.3–124.2) | 120.2±1.9 (117.3–124) | 120.2±1.9 (117.3–124) | 121.5±1.8 (118.8–126) | 121.3±2.1 (119.1–126) | 121.6±1.5 (119.1–126) |                      |                      |                      |                      |                      |
| HL (mm)                              | 35.1                 | 43.5±6.5 (27.9–55.9)  | 47.5±3.4 (42–55.9)      | 47.4±2.8 (42.6–50.9)    | 47.7±4.2 (42–55.9)    | 47.7±4.2 (42–55.9)    | 39.5±6.3 (27.9–48.8)  | 41.3±5.1 (31.4–48.2)  | 38.3±6.9 (27.9–48.8)  |                      |                      |                      |                      |                      |
| <b>Percentage of head length</b>     |                      |                       |                         |                         |                       |                       |                       |                       |                       |                      |                      |                      |                      |                      |
| SN                                   | 19.9                 | 23.6±1.9 (18.2–27)    | 24.3±1.6 (18.2–27)      | 24.2±2 (18.2–27)        | 24.5±1.1 (23–26.5)    | 24.5±1.1 (23–26.5)    | 22.8±1.9 (18.5–26.4)  | 23.2±2.1 (21.4–25.5)  | 22.5±2.2 (18.5–26.4)  |                      |                      |                      |                      |                      |
| ED                                   | 25.8                 | 23.6±2 (19.9–27.6)    | 22.4±1.4 (19.9–25.9)    | 22.8±1.3 (20.9–25.9)    | 22±1.5 (19.9–24.7)    | 22±1.5 (19.9–24.7)    | 24.8±1.7 (21.2–27.6)  | 24.9±1 (22.9–26.6)    | 24.8±2.1 (21.2–27.6)  |                      |                      |                      |                      |                      |
| EC                                   | 31.8                 | 27.6±2.2 (23.2–33)    | 26.3±1.6 (23.2–29)      | 26.6±1.5 (23.6–29)      | 25.9±1.7 (23.2–28.6)  | 25.9±1.7 (23.2–28.6)  | 29.1±0.9 (25.3–33)    | 29.1±0.9 (27.5–30.6)  | 28.9±2.4 (25.3–33)    |                      |                      |                      |                      |                      |
| EH                                   | 25.8                 | 23.4±1.6 (19.7–26.3)  | 22.4±1.3 (19.7–25.3)    | 22.6±1.2 (20.8–25.3)    | 22.1±1.4 (19.7–25)    | 22.1±1.4 (19.7–25)    | 24.4±1.2 (22.1–26.3)  | 24.4±1.2 (22.8–26.2)  | 24.4±1.4 (22.1–26.3)  |                      |                      |                      |                      |                      |
| ES                                   | 3.6                  | 4.3±1.2 (1.7–6.8)     | 3.6±1.1 (1.7–5.9)       | 3.3±0.9 (1.7–5.2)       | 4.1±1.1 (2.1–5.9)     | 4.1±1.1 (2.1–5.9)     | 4.9±0.9 (3.4–6.8)     | 4.9±0.8 (4.0–6.8)     | 4.9±1.1 (3.4–6.5)     |                      |                      |                      |                      |                      |

| Morphological characters | <i>C. fittoid</i><br>Lectotype | Both lakes           |                  |                     | Lake Thun   |                  |                     | Lake Brienz      |                  |                     |             |                  |                     |                  |             |                     |             |                  |                     |                |             |
|--------------------------|--------------------------------|----------------------|------------------|---------------------|-------------|------------------|---------------------|------------------|------------------|---------------------|-------------|------------------|---------------------|------------------|-------------|---------------------|-------------|------------------|---------------------|----------------|-------------|
|                          |                                | Non-types both sexes |                  |                     | Non-types   |                  |                     | Non-types        |                  |                     |             |                  |                     |                  |             |                     |             |                  |                     |                |             |
|                          |                                | <i>N</i>             | Mean $\pm$ StDev | Range               | <i>N</i>    | Mean $\pm$ StDev | Range               | <i>N</i>         | Mean $\pm$ StDev | Range               | <i>N</i>    | Mean $\pm$ StDev | Range               |                  |             |                     |             |                  |                     |                |             |
|                          |                                |                      |                  | <i>N</i> total = 60 |             |                  | <i>N</i> total = 17 |                  |                  | <i>N</i> total = 13 |             |                  | <i>N</i> total = 30 |                  |             | <i>N</i> total = 12 |             |                  | <i>N</i> total = 18 |                |             |
|                          |                                |                      |                  | Mean $\pm$ StDev    | Range       | Mean $\pm$ StDev | Range               | Mean $\pm$ StDev | Range            | Mean $\pm$ StDev    | Range       | Mean $\pm$ StDev | Range               | Mean $\pm$ StDev | Range       | Mean $\pm$ StDev    | Range       | Mean $\pm$ StDev | Range               |                |             |
| PostO                    | 49.8                           | 51.3 $\pm$ 1.8       | (46.8-54.8)      | 52.2 $\pm$ 1.4      | (48.7-54.8) | 52.2 $\pm$ 1.1   | (48.7-54.8)         | 52.2 $\pm$ 1.1   | (48.7-54.8)      | 50.5 $\pm$ 1.7      | (46.8-54)   | 50.7 $\pm$ 1     | (49.8-53)           | 50.3 $\pm$ 2.1   | (46.8-54)   | 50.3 $\pm$ 2.1      | (46.8-54)   | 50.3 $\pm$ 2.1   | (46.8-54)           | 50.3 $\pm$ 2.1 | (46.8-54)   |
| HD                       | 68.3                           | 69.6 $\pm$ 3.1       | (63.6-78.6)      | 70.7 $\pm$ 3.3      | (65.5-78.6) | 70.8 $\pm$ 2.7   | (66.3-74.8)         | 70.8 $\pm$ 2.7   | (66.3-74.8)      | 68.5 $\pm$ 2.6      | (63.7-73.2) | 68.8 $\pm$ 2.8   | (65.7-73.2)         | 68.3 $\pm$ 2.5   | (63.6-72.2) | 68.3 $\pm$ 2.5      | (63.6-72.2) | 68.3 $\pm$ 2.5   | (63.6-72.2)         | 68.3 $\pm$ 2.5 | (63.6-72.2) |
| MW                       | 11.5                           | 10.1 $\pm$ 0.8       | (8.2-12.1)       | 10.0 $\pm$ 0.9      | (8.2-12.1)  | 9.8 $\pm$ 0.9    | (8.2-11.4)          | 9.8 $\pm$ 0.9    | (8.2-11.4)       | 10.1 $\pm$ 0.8      | (8.5-11.4)  | 10.0 $\pm$ 0.9   | (8.5-11.4)          | 10.2 $\pm$ 0.8   | (8.6-11.4)  | 10.2 $\pm$ 0.8      | (8.6-11.4)  | 10.2 $\pm$ 0.8   | (8.6-11.4)          | 10.2 $\pm$ 0.8 | (8.6-11.4)  |
| UJ                       | 30.5                           | 30.2 $\pm$ 1.4       | (27.6-34.1)      | 30.5 $\pm$ 1.5      | (28-34.1)   | 30.8 $\pm$ 1.6   | (28-34.1)           | 30.8 $\pm$ 1.6   | (28-34.1)        | 30.2 $\pm$ 1.3      | (28.2-33.1) | 29.5 $\pm$ 1.3   | (27.6-32)           | 29.6 $\pm$ 1.3   | (27.6-32)   | 29.6 $\pm$ 1.3      | (27.6-32)   | 29.6 $\pm$ 1.3   | (27.6-32)           | 29.6 $\pm$ 1.3 | (27.6-32)   |
| Lj                       | 38.4                           | 41.6 $\pm$ 2.6       | (36.9-48.4)      | 40.7 $\pm$ 2.1      | (36.9-46.1) | 41.3 $\pm$ 2.1   | (37.4-46.1)         | 39.8 $\pm$ 1.8   | (36.9-42.3)      | 39.8 $\pm$ 1.8      | (36.9-42.3) | 42.6 $\pm$ 2.6   | (40.6-47.8)         | 42.2 $\pm$ 2.9   | (37.6-48.4) | 42.2 $\pm$ 2.9      | (37.6-48.4) | 42.2 $\pm$ 2.9   | (37.6-48.4)         | 42.2 $\pm$ 2.9 | (37.6-48.4) |
| M                        | 26.6                           | 21.8 $\pm$ 1.3       | (18.5-25.6)      | 21.8 $\pm$ 1.6      | (18.5-25.6) | 22.1 $\pm$ 1.4   | (19.8-25.6)         | 22.1 $\pm$ 1.4   | (19.8-25.6)      | 21.5 $\pm$ 1.7      | (18.5-25.1) | 21.7 $\pm$ 1     | (18.7-24.2)         | 21.5 $\pm$ 1.1   | (18.7-24.2) | 21.5 $\pm$ 1.1      | (18.7-24.2) | 21.5 $\pm$ 1.1   | (18.7-24.2)         | 21.5 $\pm$ 1.1 | (18.7-24.2) |
| SD                       | 8.1                            | 9.3 $\pm$ 1.2        | (6.7-12.4)       | 9.5 $\pm$ 1.2       | (6.7-12.4)  | 9.1              | (6.7-10.5)          | 10.1 $\pm$ 1.1   | (8.7-12.4)       | 9.1                 | (6.7-10.5)  | 9.4 $\pm$ 1.2    | (6.9-10.9)          | 8.8 $\pm$ 1      | (6.7-10.4)  | 8.8 $\pm$ 1         | (6.7-10.4)  | 8.8 $\pm$ 1      | (6.7-10.4)          | 8.8 $\pm$ 1    | (6.7-10.4)  |
| SW                       | 15                             | 17.7 $\pm$ 1.3       | (14.7-20.4)      | 17.5 $\pm$ 1.3      | (14.7-20.4) | 17.6 $\pm$ 1.5   | (14.7-20.4)         | 17.5 $\pm$ 1.1   | (16-19.6)        | 17.8 $\pm$ 1.3      | (14.7-19.7) | 17.4 $\pm$ 1.6   | (14.7-19.7)         | 18 $\pm$ 1.1     | (15.8-19.7) | 18 $\pm$ 1.1        | (15.8-19.7) | 18 $\pm$ 1.1     | (15.8-19.7)         | 18 $\pm$ 1.1   | (15.8-19.7) |
| HW                       | 45.2                           | 49.8 $\pm$ 3.1       | (42.3-57.2)      | 51.1 $\pm$ 3        | (45.8-56.6) | 51.5 $\pm$ 3.4   | (45.8-56.6)         | 50.6 $\pm$ 2.3   | (47.8-54.1)      | 48.5 $\pm$ 2.7      | (42.3-57.2) | 48.8 $\pm$ 3.5   | (42.3-57.2)         | 48.3 $\pm$ 2     | (44.8-52.8) | 48.3 $\pm$ 2        | (44.8-52.8) | 48.3 $\pm$ 2     | (44.8-52.8)         | 48.3 $\pm$ 2   | (44.8-52.8) |
| IGW                      | 24.5                           | 27.1 $\pm$ 1.5       | (22.8-31.5)      | 27.2 $\pm$ 1.6      | (23.6-31.5) | 27.2 $\pm$ 1.4   | (23.6-29.7)         | 26.8 $\pm$ 1.6   | (25.4-31.5)      | 26.4 $\pm$ 1.1      | (22.8-28.8) | 26.6 $\pm$ 0.9   | (25.4-28.8)         | 26.2 $\pm$ 1.3   | (22.8-28.5) | 26.2 $\pm$ 1.3      | (22.8-28.5) | 26.2 $\pm$ 1.3   | (22.8-28.5)         | 26.2 $\pm$ 1.3 | (22.8-28.5) |
| INW                      | 10.9                           | 11.5 $\pm$ 1.1       | (9.2-13.5)       | 11.7 $\pm$ 1        | (9.8-13.5)  | 11.6 $\pm$ 1.1   | (9.8-13.3)          | 11.8 $\pm$ 0.9   | (10.6-13.5)      | 11.4 $\pm$ 1.2      | (9.2-13.5)  | 11.2 $\pm$ 1     | (10.1-13.3)         | 11.5 $\pm$ 1.3   | (9.2-13.5)  | 11.5 $\pm$ 1.3      | (9.2-13.5)  | 11.5 $\pm$ 1.3   | (9.2-13.5)          | 11.5 $\pm$ 1.3 | (9.2-13.5)  |
| LjW                      | 14.7                           | 12 $\pm$ 1.9         | (7.9-16)         | 12.4 $\pm$ 2.3      | (7.9-16)    | 12.5 $\pm$ 2.2   | (7.9-15.8)          | 12.4 $\pm$ 2.5   | (7.9-16)         | 11.6 $\pm$ 1.2      | (8.6-13.3)  | 11.4 $\pm$ 1.3   | (8.7-13.3)          | 11.8 $\pm$ 1.2   | (8.6-13.2)  | 11.8 $\pm$ 1.2      | (8.6-13.2)  | 11.8 $\pm$ 1.2   | (8.6-13.2)          | 11.8 $\pm$ 1.2 | (8.6-13.2)  |
| UjW                      | 23.7                           | 24 $\pm$ 1.8         | (20.3-30.3)      | 24.7 $\pm$ 1.8      | (21-30.3)   | 25.2 $\pm$ 2     | (21-30.3)           | 25.2 $\pm$ 2     | (21-30.3)        | 24.1 $\pm$ 1.3      | (22.1-26.8) | 23.4 $\pm$ 1.5   | (20.3-26.5)         | 23.5 $\pm$ 1.5   | (21-26)     | 23.5 $\pm$ 1.5      | (21-26)     | 23.5 $\pm$ 1.5   | (21-26)             | 23.5 $\pm$ 1.5 | (21-26)     |
| MGR                      | 14.3                           | 14.5 $\pm$ 2         | (10.5-21.3)      | 15.8 $\pm$ 1.9      | (12.5-21.3) | 16.3 $\pm$ 1.8   | (13.9-21.3)         | 15 $\pm$ 1.8     | (12.5-19.6)      | 13.2 $\pm$ 1.2      | (10.5-15)   | 13 $\pm$ 1       | (11.5-14.4)         | 13.3 $\pm$ 1.4   | (10.5-15)   | 13.3 $\pm$ 1.4      | (10.5-15)   | 13.3 $\pm$ 1.4   | (10.5-15)           | 13.3 $\pm$ 1.4 | (10.5-15)   |
| IJR                      | 14.9                           | 15.6 $\pm$ 2.1       | (12.3-22.6)      | 16.9 $\pm$ 2        | (12.8-22.6) | 17.5 $\pm$ 1.9   | (15.4-22.6)         | 16.1 $\pm$ 1.9   | (12.8-19.6)      | 14.3 $\pm$ 1.1      | (12.3-16.4) | 14.3 $\pm$ 0.9   | (12.7-15.5)         | 14.3 $\pm$ 1.2   | (12.3-16.4) | 14.3 $\pm$ 1.2      | (12.3-16.4) | 14.3 $\pm$ 1.2   | (12.3-16.4)         | 14.3 $\pm$ 1.2 | (12.3-16.4) |
| UA                       | 19                             | 18.6 $\pm$ 1.5       | (15.7-22.6)      | 19.1 $\pm$ 1.6      | (16.1-22.6) | 18.6 $\pm$ 1.4   | (16.1-21.2)         | 19.7 $\pm$ 1.7   | (17.3-22.6)      | 18.2 $\pm$ 1.1      | (15.7-20.1) | 18 $\pm$ 0.8     | (16.7-19.4)         | 18.4 $\pm$ 1.3   | (15.7-20.1) | 18.4 $\pm$ 1.3      | (15.7-20.1) | 18.4 $\pm$ 1.3   | (15.7-20.1)         | 18.4 $\pm$ 1.3 | (15.7-20.1) |
| LA                       | 35.3                           | 35.8 $\pm$ 1.8       | (32.5-41.3)      | 35.9 $\pm$ 1.7      | (32.5-41.3) | 36.1 $\pm$ 1.4   | (34-38.6)           | 35.7 $\pm$ 2.1   | (32.5-41.3)      | 35.7 $\pm$ 1.9      | (32.9-39.8) | 35.7 $\pm$ 1.2   | (33.4-37.3)         | 35.8 $\pm$ 2.3   | (32.9-39.8) | 35.8 $\pm$ 2.3      | (32.9-39.8) | 35.8 $\pm$ 2.3   | (32.9-39.8)         | 35.8 $\pm$ 2.3 | (32.9-39.8) |
| Meristic characters      |                                | Mode                 | Range            | Mode                | Range       | Mode             | Range               | Mode             | Range            | Mode                | Range       | Mode             | Range               | Mode             | Range       | Mode                | Range       | Mode             | Range               | Mode           | Range       |
| PelF                     | 1                              | 1                    | (1-1)            | 1                   | (1-1)       | 1                | (1-1)               | 1                | (1-1)            | 1                   | (1-1)       | 1                | (1-1)               | 1                | (1-1)       | 1                   | (1-1)       | 1                | (1-1)               | 1              | (1-1)       |
| PelF unbranched          |                                |                      |                  |                     |             |                  |                     |                  |                  |                     |             |                  |                     |                  |             |                     |             |                  |                     |                |             |
| PelF branched            | 11                             | 10                   | (9-11)           | 10                  | (9-11)      | 10               | (9-11)              | 10               | (9-11)           | 10                  | (9-11)      | 10               | (10-11)             | 10               | (9-11)      | 10                  | (10-11)     | 10               | (10-11)             | 10             | (9-11)      |
| PelF unbranched          |                                |                      |                  |                     |             |                  |                     |                  |                  |                     |             |                  |                     |                  |             |                     |             |                  |                     |                |             |
| PelF branched            | 16                             | 16                   | (14-17)          | 16                  | (14-17)     | 16               | (14-17)             | 16               | (15-17)          | 16                  | (14-17)     | 16               | (14-17)             | 16               | (14-17)     | 16                  | (14-17)     | 16               | (14-17)             | 16             | (14-17)     |
| DF unbranched            | 4                              | 4                    | (3-4)            | 4                   | (3-4)       | 4                | (3-4)               | 4                | (3-4)            | 4                   | (3-4)       | 4                | (3-4)               | 4                | (3-4)       | 4                   | (3-4)       | 4                | (3-4)               | 4              | (3-4)       |
| DF branched              | 10                             | 10                   | (10-13)          | 10                  | (10-11)     | 10               | (10-11)             | 10               | (10-11)          | 10                  | (10-11)     | 11               | (10-13)             | 11               | (10-12)     | 11                  | (10-12)     | 11               | (10-12)             | 11             | (10-13)     |
| AF unbranched            | 3                              | 3                    | (2-5)            | 3                   | (2-4)       | 3                | (2-4)               | 3                | (2-4)            | 3                   | (2-4)       | 3                | (3-5)               | 3                | (3-4)       | 3                   | (3-5)       | 3                | (3-4)               | 3              | (3-4)       |
| AF branched              | 12                             | 12                   | (10-14)          | 12                  | (10-14)     | 12               | (11-14)             | 12               | (10-14)          | 12                  | (11-14)     | 12               | (11-13)             | 12               | (11-13)     | 12                  | (11-13)     | 12               | (11-13)             | 12             | (11-13)     |
| LS                       | 82                             | 86                   | (78-93)          | 86                  | (78-93)     | 85               | (78-86)             | 86               | (78-93)          | 86                  | (79-92)     | 86               | (81-92)             | 86               | (79-91)     | 86                  | (81-92)     | 86               | (81-92)             | 86             | (79-91)     |
| PDS                      | 32                             | 36                   | (30-44)          | 32                  | (30-44)     | 36               | (30-40)             | 38               | (31-44)          | 34                  | (30-38)     | 34               | (30-38)             | 34               | (30-38)     | 34                  | (30-38)     | 34               | (30-38)             | 34             | (33-40)     |
| TDS                      | 10                             | 9                    | (8-11)           | 9                   | (8-11)      | 9                | (9-10)              | 10               | (8-11)           | 10                  | (9-10)      | 10               | (9-10)              | 10               | (9-10)      | 10                  | (9-10)      | 10               | (9-10)              | 10             | (9-10)      |
| TAS                      | 7                              | 8                    | (7-10)           | 8                   | (7-9)       | 8                | (7-9)               | 8                | (7-9)            | 8                   | (7-9)       | 8                | (8-9)               | 8                | (7-9)       | 8                   | (8-9)       | 8                | (8-9)               | 8              | (7-9)       |
| TPS                      | 8                              | 9                    | (7-10)           | 9                   | (7-9)       | 9                | (8-9)               | 9                | (8-9)            | 9                   | (8-9)       | 9                | (8-9)               | 9                | (8-9)       | 9                   | (8-9)       | 9                | (8-9)               | 9              | (8-9)       |
| UGR                      | 11                             | 12                   | (10-16)          | 14                  | (10-16)     | 14               | (12-16)             | 14               | (10-15)          | 12                  | (11-15)     | 12               | (11-14)             | 12               | (11-15)     | 12                  | (11-14)     | 12               | (11-14)             | 12             | (11-15)     |
| IJR                      | 22                             | 24                   | (19-27)          | 24                  | (22-27)     | 24               | (22-27)             | 24               | (22-26)          | 22                  | (19-27)     | 22               | (22-26)             | 24               | (19-27)     | 22                  | (22-26)     | 24               | (22-26)             | 24             | (19-27)     |
| total GR                 | 33                             | 38                   | (32-43)          | 38                  | (32-43)     | 38               | (34-43)             | 38               | (32-40)          | 35                  | (32-40)     | 37               | (33-38)             | 39               | (32-40)     | 39                  | (33-38)     | 39               | (33-38)             | 39             | (32-40)     |

*Coregonus* “Large type”: Maurer and Guthruf 2005; Müller et al. 2007 (see also synonymy of *C. alpinus* and *C. brienzii*)

*Coregonus lavaretus wartmanni* natio *fatioi*: Berg 1932

*Coregonus lavaretus* natio *arurensis*, oekot. *pelagicus*: Steinmann 1950 (see also synonymy of *C. steinmanni*)

*Coregonus lavaretus* natio *arurensis*, oekot. *primigenius*: Steinmann 1950 (see also synonymy of *C. steinmanni* and *C. alpinus*)

*Coregonus* “Bodenalbock”, “Albock”, “Schwebalbock”, “Wanderalbock”: Steinmann 1950 (see also synonymy of *C. alpinus*, *C. steinmanni*)

*Coregonus* sp. “Felchen”: Hudson et al. 2011, 2013, 2016; Ingram et al. 2012

*Coregonus* sp. “Tiefenalbock”: Vonlanthen et al. 2015

*Coregonus wartmanni alpinus*: Fatio 1890

**Material examined. Lectotype.** MHNG-809.059, Switzerland, Lake Thun (46°40'N, 7°46'E), 154.5 mm SL, sex unknown.

**Non-types.** NMBE-1077133, NMBE-1077180–1077185, NMBE-1077135–1077157, Switzerland, Lake Thun (46°40'N, 7°46'E), N = 30, 191–288 mm SL; NMBE-1077342, NMBE-1077291–1077317, NMBE-1077266, NMBE-1077267, Switzerland, Lake Brienz (46°43'N, 7°57'E), N = 30, 132–244 mm SL.

**Diagnosis.** *Coregonus fatioi* is a medium-sized whitefish with weak pigmentation of all fins and body; light to dark green colour on the flanks above the lateral line; moderate to many pigmented small dots on the scales along the flank and the dorsum; slender, elongated and slightly torpedo-like body; long head; tip of snout is fleshy and roundish; small eye with a thin and triangular to roundish eye socket for individuals from Lake Thun and a thick and triangular shaped eye socket for individuals from Lake Brienz; many and long gill rakers.

**Differential diagnosis.** Differential diagnoses against *C. albellus* and *C. alpinus* are given under those species' accounts.

#### ***Coregonus fatioi*-*Coregonus brienzii***

In Brienz *C. fatioi* can be differentiated from *C. brienzii* by being deeper bodied (22.1–26.2% SL, mean = 23.9 vs. 19.6–25.1% SL, mean = 22.6) and having a smaller eye (eye depth: 21.2–27.6% HL, mean = 24.8 vs. 23.1–28.3% SL, mean = 25.3) (Tables 5, 7, 11).

#### ***Coregonus fatioi*-*Coregonus steinmanni***

The specimens of *C. fatioi* from Lake Thun differ from those of *C. steinmanni* by having longer gill rakers (middle gill raker length: 12.5–21.3% HL, mean = 15.8 vs. 9.1–14.3% HL, mean = 11.5; longest gill raker length: 12.8–22.6% HL, mean = 16.9 vs. 10–14.4% HL, mean = 12.1), a longer and wider underjaw (under jaw length: 28–34.1% HL, mean = 30.5 vs. 25.2–30% HL, mean = 27.3; under jaw width: 21–30.3% HL, mean = 24.7 vs. 19.3–25% HL, mean = 23). Based on ratios *C. fatioi* can be differentiated from *C. steinmanni* by having a smaller “caudal peduncle depth / upper jaw length” ratio (CD/UJ: 1.02–1.34 vs. 1.36–1.55) and “caudal peduncle depth / postdorsal length” ratio (CD/PostD: 0.14–0.17 vs. 0.17–0.20) (Tables 5, 6, 10).



**Figure 6.** *Coregonus fatioi*, lakes Thun and Brienz, Switzerland **A, B** lectotype, MHNG-809.059, Lake Thun, 154.5 mm SL, sex unknown, left and right side of the specimen **C** non-type, NMBE-1077139, Lake Thun, 240 mm SL, male, freshly caught specimen **D** non-type, NMBE-1077317, Lake Brienz, 202 mm SL, male, frozen and defrosted specimen. The white scale (1 cm) below each fish acts as a reference for the actual size of the specimen.

***Coregonus fatioi*–*Coregonus profundus***

*Coregonus fatioi* from Lake Thun can be distinguished from *C. profundus* by having more and longer gill rakers (upper arch gill raker number: 10–16, mode = 14 vs. 5–10, mode = 9; lower arch gill raker number: 22–27, mode = 24 vs. 10–18, mode = 14; total gill raker number: 32–43, mode = 38 vs. 15–27, mode = 21; middle gill raker length: 12.5–21.3% HL, mean = 15.8 vs. 7.6–11.7% HL, mean = 9.2; longest gill raker length: 12.8–22.6% HL, mean = 16.9 vs. 7.8–12.4% HL, mean = 10.1), shorter pectoral fin (pectoral fin 1 length: 13.3–18.9% SL, mean = 16.5 vs. 16.6–21% SL, mean = 18.4; pectoral fin 2 length: 13.8–20.6% SL, mean = 17.7 vs. 17.7–23.2% SL, mean = 20.2), a shorter head (13.6–16.2% SL, mean = 14.8 vs. 15.5–18.4% SL, mean = 16.4), a longer postdorsal length (41.6–50.7% SL, mean = 44.9 vs. 38.9–44.5% SL, mean = 42.5), and a longer upper jaw (28–34.1% HL, mean = 30.5 vs. 26.4–30.6% HL, mean = 28.7) (Tables 5, 8, Suppl. material 1: Table S6).

***Coregonus fatioi*–*Coregonus acrinus***

*Coregonus fatioi* can be distinguished from *C. acrinus* by having a longer postdorsal length (41.6–50.7% SL, mean = 44.9 vs. 40.3–45.6% SL, mean = 43) and longer gill rakers (middle gill raker length: 12.5–21.3% HL, mean = 15.8 vs. 9.1–16.6% HL, mean = 13.4; longest gill raker length: 12.8–22.6% HL, mean = 16.9 vs. 11.4–16.9% HL, mean = 14.5) (Tables 5, 9).

**Description.** General appearance is shown in Figure 6. Morphological and meristic characters of both sexes can be found in Table 5 and Suppl. material 1: Table S6 and first- and second-best ratios for both sexes combined can be found in Tables 10, 11. The description is valid for both sexes and both lakes; differences between the populations of lakes Thun and Brienz are mentioned.

**Shape:** Elongated. Slender bodied with greatest body depth anterior of the dorsal fin resulting in a slightly torpedo-like form. Dorsal and ventral profile similar and slightly arched. Dorsal and ventral profile from tip of snout to interorbital area mostly straight and then slightly convex to dorsal and pelvic fin origin respectively. Head long. Very rarely does the snout have an approx. 40–50° angle to the body axis anterior of the eye, such that the profile from the tip of the snout to the vertical projection where the anterior part of the eye crosses the dorsal profile is straight and afterwards slightly convex. Mouth thick (i.e., width of upper and lower jaw), long and often terminal and only rarely slightly sub-terminal. Snout mostly wider than deep, not strongly pronounced, since the tip of the snout is often fleshy and roundish. Specimens from Lake Thun have a thin, roundish and rarely triangular shaped eye-socket, whereas specimens from Lake Brienz have an eye-socket that is thick and triangular (i.e., sickle-shaped). Pectoral fin moderately tapered. Anterior unbranched ray of the erected dorsal fin ranges from almost vertically straight to an approx. 60–80° angle to body axis and only bent slightly posteriorly at the end of the ray. Caudal peduncle narrow and elongated with caudal fin forked in specimens from both lakes and sometimes moderately asymmetrical (mostly the ventral part is longer) in specimens from Lake Thun but very rarely in specimens from Lake Brienz. Unbranched ray of anal fin straight and rarely bent posteriorly at the end of the ray. Anal fin longest anteriorly and progres-

sively shortening posteriorly with the outer margin of the anal fin ranging from being straight to slightly concave.

**Meristics:** Specimens of Lake Thun have many and long gill rakers, whereas specimens from Lake Brienz have a bit less and moderately long gill rakers.

**Colour:** Pigmentation of fins and body overall weak in live specimens. In specimens from Lake Thun the pectoral fin is translucent, sometimes yellowish with faint pigmentation at the median to distal parts of the fin. In Thun the pelvic fin ranges from completely translucent to moderately pigmented and the dorsal, adipose, anal and caudal fins are moderately pigmented. Specimens from Lake Brienz have a fully translucent pectoral fin that sometimes has a faint pigmentation on the unbranched ray. Pelvic and anal fins range from fully transparent to moderately pigmented and dorsal, adipose and caudal fins are moderately pigmented. In both lakes fish have a silvery appearance along the flanks. Specimens from both lakes sometimes have many pigmented small dots on the scales along the flank and the dorsum, which is rare in specimens from Lake Thun and common in specimens from Lake Brienz. Distribution of the dots is bound to the scale patterning such that the dots are found at the edge of the scales or at the boundary point of two scales (as can be found for the species of *C. alpinus*, *C. brienzii* and *C. steinmanni*). Colouration on the dorsum above the lateral line of specimens from Lake Thun ranges from a light green colouration (e.g., RGB (136, 245, 205)) to an olive-green colouration (e.g., RGB (176, 192, 125)), where the former is more common. In specimens from Lake Brienz the upper dorsum is light greenish in colouration (e.g., RGB (136, 245, 205)). For a comparison to the main colouration found in the other species see Suppl. material 1: Figure S8. The dorsal part of the head of specimens of Lake Brienz is weakly pigmented, whereas that of specimens from Lake Thun is moderately pigmented. The snout around the nostrils is weakly (Lake Brienz) to moderately (Lake Thun) pigmented with a gap of very weak (Brienz) to moderate (Thun) pigmentation posteriorly of the nostrils up to the height of the middle of the eyes. Operculum and pre-operculum are silvery with one black dot on the lower margin of the pre-operculum. Preserved specimens are pale in colouration with similar pigmentation as described for live specimens. Silvery, translucent, not coloured or unpigmented parts of the body become brown-yellowish (e.g., RGB (239, 210, 40)), whereas the pigmented parts are conserved and the coloured parts (dorsally above the lateral line) become brownish (e.g., RGB (186, 140, 100)).

**Distribution and notes on biology.** *Coregonus fatioi* is found in the lakes Thun (46°40'N, 7°46'E) and Brienz (46°43'N, 7°57'E) that are connected through the river Aare at Interlaken. Based on isotopic signatures *C. fatioi* feeds predominantly on zooplankton (Selz 2008; Hudson 2011; Ingram et al. 2012). Stomach content analyses of specimens of *C. fatioi* from Lake Brienz suggest that *C. fatioi* feeds on a mix of zooplankton and benthic prey (Maurer and Guthruf 2005; Müller et al. 2007). *Coregonus fatioi* has a moderately fast growth rate (Both lakes: Kirchhofer 1995; Bittner et al. unpublished; Lake Brienz: Müller et al. 2007). It has to be noted that the work by Kirchhofer (1995), Maurer and Guthruf (2005) and Müller et al. (2007) did not

distinguish between all species in lakes Thun or Brienz and thus lumped different species together into few groups. Maurer and Guthruf (2005) and Müller et al. (2007) differentiated between “small-type” and “large-type” whitefish based on cohort-specific threshold values for length-at-age. Based on morphology and ecology Kirchhofer (1995) differentiated in Lake Thun between “Albock” (comprising most likely of *C. alpinus*, *C. steinmanni* and *C. acrinus*), “Brienzig” (comprising most likely of *C. albellus* and *C. fatioi*) and “Kropfer” (*C. profundus*) and in Lake Brienz between “Felchen” (comprising most likely of *C. alpinus*, *C. fatioi* and *C. brienzi*) and “Brienzig” and “Winter-Brienzig” (comprising of summer- and winter-spawning specimens of *C. albellus*). The gill raker number and length of *C. fatioi* (many and long gill rakers) suggests, based on the functional properties of the number of gill rakers (Lundsgaard-Hansen et al. 2013; Roesch et al. 2013), that *C. fatioi* feeds more on zooplankton and less on benthic prey. However, this assumption needs to be verified with stomach content analyses that distinguish between the different species within a lake. Habitat stratified random sampling of Lake Thun (mid-October 2013; Vonlanthen et al. 2015) and Brienz (mid-September 2011; Vonlanthen et al. 2013) shows, that *C. fatioi* occupies the moderately shallow (Brienz: approx. 1–48 m,  $N = 9$ ; Thun: approx. 25–140 m,  $N = 4$ ) to the deepest waters of the benthic habitat in both lakes (down to 217 m and 261 m in lakes Thun and Brienz, respectively) (Dönz et al. 2018). In the pelagic habitat *C. fatioi* aggregates in lakes Thun and Brienz in moderate water depths (Brienz: approx. 1–100 m,  $N = 10$ ; Thun: approx. 10–40 m,  $N = 9$ ) (Dönz et al. 2018). Note that the habitat-stratified random sampling data for both lakes only covers a short period of time (one month in late summer) and it is thus not clear how the species are distributed spatially through the rest of the year. Furthermore, the habitat-stratified random sampling in the both lakes did not distinguish between ripe and unripe specimens, and thus in the case of *C. fatioi* the distribution pattern along the depth in the benthic zone is biased by the spawning aggregation of this species since the sampling period in both lakes coincides partially with the spawning season of this species. *Coregonus fatioi* resembles phenotypically *C. albellus* and to some extent *C. profundus*. Interestingly, Steinmann (1950) already mentioned for Lake Thun that the ecotype “*Coregonus lavaretus* L. nat. arurenis, oekot. nanus” (most likely *C. albellus*) should be grouped based on its ecology closely to the ecotype “*Coregonus lavaretus* L. nat. arurenis, oekot. pelagicus” (most likely *C. fatioi*). Steinmann mentions the German name “Schwebalbock” for the ecotype “pelagicus”, which means verbally translated the “floating whitefish” and mentions that the “nanus” ecotype seems to be a small species with similar ecological properties. For the large whitefish species in Lake Thun, Steinmann (1950) defined one central ecotype, the “primigenius” ecotype, which he places – based on the size – with two other ecotypes namely the “litoralis” ecotype (most likely *C. alpinus*) and the “pelagicus” ecotype (most likely *C. fatioi*). Besides referring to a “primigenius” ecotype, Steinmann (1950) also refers to a “primigenius”-group, which most likely comprises of the “pelagicus” and “litoralis” ecotypes. A further indication of this is that he also mentions that yet another ecotype, namely the “profundus” ecotype, can be directly deduced from the

“primigenius” ecotype. Steinmann (1950) further mentions that specimens, which he places in the “primigenius”-group, used to migrate before the construction of water gates (see below) upstream from Lake Thun into the river Aare, which connects Lake Thun with Lake Brienz. Steinmann (1950) mentions that these fish belong to the “primigenius”-group, but did not specify if the migrating population constituted of individuals of the “litoralis” or the “pelagicus” ecotype or both. This migrating population was referred to as “Wanderlbock” (i.e. migrating whitefish) in German and historically migrated from Lake Thun into Lake Brienz during the spawning season, before migration became impossible due to the construction of water gates in 1856 (Fatio 1890; Dönz et al. 2018). Fatio (1890) mentioned that a large part of the population of *C. fatioi* “disappeared” at the beginning of the spawning season in late August and was caught by fishermen in the river Aare downstream (near the city of Thun or Bern) or upstream (near the city of Interlaken) of Lake Thun before and after the construction of the water gate. We compared six whitefish specimens from the museum collections of the MHNG and NMBE, which had no species designation but where it was mentioned that they were caught in the river Aare near the city of Bern (in the years 1881 and 1895), Thun (in the year 1950) and Interlaken (in the year 1945), to the contemporary specimens of Lake Thun including the type specimens of *C. albellus*, *C. fatioi* and *C. alpinus*. All the specimens were caught after the construction of the water gate, when free movement between the lakes was already constrained. All six specimens from the river Aare group in morphospace within the range or adjacent to the range of the contemporary specimens of *C. fatioi* including the type specimen (Suppl. material 1: Figure S11a–c), suggesting that the historically migrating population of whitefish from Lake Thun most likely belonged to the species *C. fatioi*. Bittner (2009) sampled and genotyped individuals of a population of whitefish spawning in the river Aare near Interlaken. Dönz et al. (2018) re-analysed those individuals and was able to assign 4 individuals with high assignment probability (>70%) to several different contemporary species of Lake Thun, namely *C. alpinus* (individual assignment probability of THL15N18 = 86%), *C. acrinus* (ind. assign. prob. of THL15N07 and THL15N23 = 77% and 80%, respectively) and *C. fatioi* (ind. assign. prob. of THL15NfS1124 = 92%). This suggest either that historically more species than just *C. fatioi* migrated to the river Aare for spawning and were missed both by Fatio (1890) and Steinmann (1950) and are thus not represented in our PCA morphospace of Aare river whitefish (Suppl. material 1: Figure S11 a–c). Or the historical migratory population consisted – as has been suggested by Fatio (1890) and Steinmann (1950) – of individuals of *C. fatioi*. The average size (total length) at 3 years of age for specimens in this study is  $266 \pm 15$  mm (mean and standard deviation,  $N = 14$ ) and  $244 \pm 14$  mm ( $N = 16$ ) for lakes Thun and Brienz respectively (Suppl. material 1: Figures S4–S6). In Lake Brienz the size of 3-year-old specimens of *C. fatioi* is considerably larger than that of *C. albellus* and similar to that of *C. alpinus* and *C. brienzi*, whereas in Lake Thun it is similar to that of *C. profundus* and *C. albellus* and smaller than that of *C. alpinus*, *C. steinmanni*, and *C. acrinus* (Suppl. material 1: Figure S6). *Coregonus fatioi* has a long spawning season with two peaks. One spawn-

ing peak is in late summer/early autumn from August to October, which seems more common in Lake Thun than Lake Brienz, and the second peak is in early to late winter from December to March (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). Spawning depth varies with spawning season and can range from approx. 40 m down to the max. depth of 210 m and 261 m in lakes Thun and Brienz, respectively (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). Occasionally *C. fatioi* can be found spawning shallower (up to 10 m), but generally it spawns in deeper waters. The spawning season and depth of *C. fatioi* partially overlaps with that of *C. steinmanni*, *C. albellus*, *C. acrinus*, and *C. profundus* in Lake Thun and with that of *C. albellus* and *C. brienzii* in Lake Brienz.

**Etymology.** The name given to this species by Fatio (1890) was preoccupied by another species described by Fatio (1885). Kottelat (1997) proposed *C. fatioi* as a replacement name. The specific epithet *fatioi* is the genitive of *Fatio*. It was named by Kottelat (1997) after the late researcher Viktor Fatio, a zoologist from Switzerland who wrote a standard reference work on the Swiss vertebrates entitled “Faune des Vertébrés de la Suisse Partie 1–3” and in which he also described part of the whitefish species diversity of Switzerland.

**Common name.** Tiefenalbock in Lake Thun and Felchen in Lake Brienz.

***Coregonus steinmanni* Selz, Dönz, Vonlanthen & Seehausen, sp. nov.**

<http://zoobank.org/C03A9DA8-8492-4CBF-B87B-406D72594530>

Figure 7

*Coregonus* “Albock”: Ruffli 1978, 1979; Kirchhofer and Tschumi 1986; Kirchhofer 1995 (see also synonymy of *C. alpinus* and *C. acrinus*)

*Coregonus* “Balchen”: Heuscher 1901; Surbeck 1917 (see also synonymy of *C. alpinus*)

*Coregonus* “Balchen”, “THU2”: Douglas et al. 1999, 2003; Douglas and Brunner 2002 (see also synonymy of *C. alpinus*)

*Coregonus lavaretus* natio *arurensis*, oekot. *primigenius*: Steinmann 1950 (see also synonymy of *C. fatioi* and *C. alpinus*)

*Coregonus* sp. “Balchen”: Hudson et al. 2011, 2013, 2016; Ingram et al. 2012; Vonlanthen et al. 2012, 2015; Vonlanthen and Périat 2013 (see also synonymy of *C. alpinus* and *C. brienzii*)

*Coregonus* sp. “Balchen 2”: Dönz et al. 2018 (see also synonymy of *C. brienzii*)

*Coregonus* “Wanderlbock”, “Bodenalbock”, “Albock”: Steinmann 1950 (see also synonymy of *C. alpinus*, *C. fatioi*, *C. steinmanni* and *C. brienzii*)

**Material examined. Holotype.** NMBE-1077219, Switzerland, Lake Thun (46°40'N, 7°46'E), 301 mm SL, female.

**Paratypes.** NMBE-1077132, NMBE-1077212–1077218, NMBE-1077220, NMBE-1077262–1077265, Switzerland, Lake Thun (46°40'N, 7°46'E), N = 13, 211–323 mm SL.

**Table 6.** Morphological and meristic data of *C. steinmanni* from Lake Thun, Switzerland, NMBE-1077219, female, holotype from Lake Thun; paratypes *N* = 12. For females and for both sexes the range and mean include the holotype.

| Morphological characters             | <i>C. steinmanni</i><br>Holotype | Lake Thun            |               |                       |               |                     |               |
|--------------------------------------|----------------------------------|----------------------|---------------|-----------------------|---------------|---------------------|---------------|
|                                      |                                  | Both sexes           |               |                       |               |                     |               |
|                                      |                                  | <i>N</i> -total = 12 |               | <i>N</i> -females = 3 |               | <i>N</i> -males = 9 |               |
|                                      |                                  | Mean ± Stdev         | Range         | Mean ± Stdev          | Range         | Mean ± Stdev        | Range         |
| SL (mm)                              | 301                              | 275.3±29.4           | (211-323)     | 276.5±36.9            | (234-301)     | 274.9±29.2          | (211-323)     |
| <b>Percentage of standard length</b> |                                  |                      |               |                       |               |                     |               |
| PelvFB                               | 4.0                              | 4.4±0.3              | (4.0-4.8)     | 4.1±0.2               | (4.0-4.3)     | 4.5±0.3             | (4.1-4.8)     |
| PelvFS                               | 5.7                              | 6.2±0.5              | (5.3-6.9)     | 6.2±0.4               | (5.7-6.5)     | 6.2±0.6             | (5.3-6.9)     |
| PelvF                                | 15.3                             | 16.5±1.1             | (14.6-18.3)   | 16.1±1.1              | (15.3-17.4)   | 16.6±1.1            | (14.6-18.3)   |
| PecFB                                | 3.2                              | 3.4±0.3              | (3.1-3.8)     | 3.2±0.2               | (3.1-3.4)     | 3.4±0.3             | (3.1-3.8)     |
| PecF1                                | 14.7                             | 16.2±1.3             | (13.9-18.2)   | 15.8±1.1              | (14.7-16.9)   | 16.4±1.4            | (13.9-18.2)   |
| PecF2                                | 15.2                             | 17±1.3               | (15.2-19.1)   | 16.2±1                | (15.2-17.2)   | 17.3±1.3            | (15.5-19.1)   |
| DFB                                  | 11.4                             | 12.6±0.8             | (11.4-13.8)   | 12.4±1.2              | (11.4-13.7)   | 12.6±0.7            | (11.7-13.8)   |
| DFAc                                 | 16.2                             | 18.8±1.7             | (16.2-21.2)   | 18.4±2.3              | (16.2-20.9)   | 19.0±1.6            | (16.2-21.2)   |
| DFAd                                 | 17.8                             | 20.1±1.6             | (17.5-22.4)   | 20.0±2.3              | (17.8-22.4)   | 20.2±1.4            | (17.5-22.1)   |
| DFPe                                 | 4.8                              | 4.8±0.7              | (3.9-6.3)     | 4.6±0.2               | (4.4-4.8)     | 4.9±0.7             | (3.9-6.3)     |
| AFB                                  | 12.1                             | 12.6±0.8             | (11.5-14.2)   | 12.6±0.5              | (12.1-13.0)   | 12.6±0.9            | (11.5-14.2)   |
| AFAc                                 | 11.2                             | 12.4±1.0             | (10.8-13.7)   | 12.3±1.3              | (11.2-13.7)   | 12.4±0.9            | (10.8-13.5)   |
| AdFB                                 | 5                                | 4.5±0.6              | (3.7-5.4)     | 4.4±0.5               | (4.0-5.0)     | 4.5±0.6             | (3.7-5.4)     |
| CF                                   | 23.6                             | 23.4±1.2             | (22.2-25.9)   | 23.7±1.2              | (22.4-24.9)   | 23.3±1.3            | (22.2-25.9)   |
| CD                                   | 7.8                              | 8±0.4                | (7.5-8.6)     | 7.9±0.2               | (7.7-8.1)     | 8±0.4               | (7.5-8.6)     |
| CL                                   | 13                               | 13.0±0.7             | (11.4-14.0)   | 13.5±0.5              | (13.0-14.0)   | 12.9±0.7            | (11.4-13.9)   |
| PAdC                                 | 18.2                             | 18±1                 | (16.4-19.6)   | 17.8±0.8              | (16.9-18.4)   | 18±1.1              | (16.4-19.6)   |
| DHL                                  | 13.6                             | 14.0±0.7             | (13.2-15.1)   | 14.3±0.7              | (13.6-14.9)   | 13.9±0.7            | (13.2-15.1)   |
| PreP                                 | 53.4                             | 51.7±1.9             | (48.6-54.3)   | 52.8±1.2              | (51.4-53.6)   | 51.3±2.0            | (48.6-54.3)   |
| PreA                                 | 78.1                             | 77.5±0.9             | (75.0-78.4)   | 78.0±0.6              | (77.4-78.4)   | 77.3±0.9            | (75.0-77.9)   |
| PreD                                 | 50                               | 47.2±1.5             | (44.5-50)     | 48.2±1.7              | (46.7-50)     | 46.9±1.4            | (44.5-49.7)   |
| BD                                   | 30                               | 27.0±1.5             | (24.6-30.0)   | 28.0±1.8              | (26.5-30.0)   | 26.7±1.3            | (24.6-28.7)   |
| PostD                                | 43.3                             | 43.3±1.2             | (41.9-45.6)   | 42.5±0.8              | (41.9-43.3)   | 43.6±1.2            | (42-45.6)     |
| TL                                   | 120.1                            | 119.6±2.3            | (115.3-122.5) | 119.5±0.6             | (118.8-120.1) | 119.6±2.7           | (115.3-122.5) |
| HL (mm)                              | 58.7                             | 55.3±4.9             | (44.8-63.3)   | 55.6±5.3              | (49.4-58.7)   | 55.2±5.1            | (44.8-63.3)   |
| <b>Percentage of head length</b>     |                                  |                      |               |                       |               |                     |               |
| SN                                   | 22.2                             | 23.2±1.7             | (20.5-26.3)   | 23.5±1.2              | (22.2-24.6)   | 23.1±1.9            | (20.5-26.3)   |
| ED                                   | 22.2                             | 22±1.1               | (20.5-24.5)   | 22.6±1.7              | (21.1-24.5)   | 21.8±0.8            | (20.5-23)     |
| EC                                   | 25.5                             | 26.2±1.2             | (24.2-27.8)   | 26.3±1.3              | (25.5-27.8)   | 26.2±1.2            | (24.2-27.4)   |
| EH                                   | 22.5                             | 21.6±1.1             | (19.6-24.1)   | 22.5±1.5              | (21-24.1)     | 21.3±0.8            | (19.6-22)     |
| ES                                   | 5.1                              | 4.8±0.6              | (3.9-5.6)     | 4.9±0.5               | (4.3-5.2)     | 4.8±0.7             | (3.9-5.6)     |
| PostO                                | 54.4                             | 52.4±1.4             | (50.3-54.4)   | 53±1.4                | (51.6-54.4)   | 52.2±1.5            | (50.3-54.3)   |
| HD                                   | 72.1                             | 72.1±2.1             | (68.9-76.3)   | 72.8±0.9              | (72.1-73.8)   | 71.8±2.4            | (68.9-76.3)   |
| MW                                   | 10.7                             | 9.3±0.7              | (8.3-10.7)    | 9.7±0.8               | (9.1-10.7)    | 9.2±0.7             | (8.3-10.6)    |
| UJ                                   | 27                               | 27.3±1.4             | (25.2-30)     | 27.3±0.7              | (26.9-28.1)   | 27.3±1.6            | (25.2-30)     |
| LJ                                   | 39.4                             | 39±1.2               | (36.6-40.4)   | 39.7±0.3              | (39.4-40)     | 38.7±1.3            | (36.6-40.4)   |
| M                                    | 19.7                             | 19.7±1.2             | (18.1-21.8)   | 19.4±0.7              | (18.6-19.9)   | 19.8±1.3            | (18.1-21.8)   |
| SD                                   | 10.4                             | 10±1.7               | (6.5-13.2)    | 10.1±0.4              | (9.7-10.4)    | 10±2                | (6.5-13.2)    |
| SW                                   | 15.8                             | 16.7±1.1             | (15.3-18.9)   | 16±0.8                | (15.3-17)     | 16.9±1.1            | (15.7-18.9)   |
| HW                                   | 53.1                             | 51.6±3.1             | (44.5-56.9)   | 49±4.3                | (44.5-53.1)   | 52.4±2.2            | (49.5-56.9)   |
| IOW                                  | 29.6                             | 27.6±2.3             | (23.8-31.2)   | 27.9±2.2              | (25.4-29.6)   | 27.5±2.4            | (23.8-31.2)   |
| INW                                  | 11.6                             | 12.1±0.7             | (11-13.2)     | 11.7±0.1              | (11.6-11.8)   | 12.3±0.7            | (11-13.2)     |
| LJW                                  | 14.3                             | 11.9±1.4             | (9.7-14.3)    | 12±2.3                | (9.7-14.3)    | 11.9±1.1            | (10.1-13.6)   |
| UJW                                  | 24.1                             | 23±1.6               | (19.3-25)     | 21.6±2.4              | (19.3-24.1)   | 23.4±1.1            | (21.2-25)     |
| MGR                                  | 11.3                             | 11.5±1.7             | (9.1-14.3)    | 11.3±1.1              | (10.2-12.4)   | 11.5±1.9            | (9.1-14.3)    |

| Morphological characters | <i>C. steinmanni</i> |                      | Lake Thun   |                       |             |                     |             |
|--------------------------|----------------------|----------------------|-------------|-----------------------|-------------|---------------------|-------------|
|                          | Holotype             | Both sexes           |             |                       |             |                     |             |
|                          |                      | <i>N</i> -total = 12 |             | <i>N</i> -females = 3 |             | <i>N</i> -males = 9 |             |
|                          |                      | Mean ± Stdev         | Range       | Mean ± Stdev          | Range       | Mean ± Stdev        | Range       |
| LGR                      | 11.7                 | 12.1±1.5             | (10-14.4)   | 11.6±1.2              | (10.4-12.9) | 12.3±1.6            | (10-14.4)   |
| UA                       | 19.6                 | 18.6±0.6             | (17.8-19.8) | 18.9±0.6              | (18.4-19.6) | 18.6±0.6            | (17.8-19.8) |
| LA                       | 34.7                 | 34.3±1.2             | (31.6-36.5) | 33.9±0.8              | (33-34.7)   | 34.4±1.3            | (31.6-36.5) |
| Meristic characters      |                      | Mode                 | Range       | Mode                  | Range       | Mode                | Range       |
| PelvF unbranched         | 1                    | 1                    | (1-1)       | 1                     | (1-1)       | 1                   | (1-1)       |
| PelvF branched           | 10                   | 10                   | (10-12)     | na                    | (10-12)     | 10                  | (10-12)     |
| PecF unbranched          | 1                    | 1                    | (1-1)       | 1                     | (1-1)       | 1                   | (1-1)       |
| PecF branched            | 15                   | 15                   | (14-16)     | na                    | (14-16)     | 15                  | (15-16)     |
| DF unbranched            | 4                    | 4                    | (3-4)       | 4                     | (3-4)       | 4                   | (3-4)       |
| DF branched              | 10                   | 10                   | (10-12)     | 10                    | (10-11)     | 10                  | (10-12)     |
| AF unbranched            | 3                    | 3                    | (3-3)       | 3                     | (3-3)       | 3                   | (3-3)       |
| AF branched              | 11                   | 12                   | (11-13)     | 12                    | (11-12)     | 12                  | (11-13)     |
| LS                       | 78                   | 78                   | (78-87)     | 78                    | (78-80)     | 85                  | (78-87)     |
| PDS                      | 40                   | 36                   | (32-40)     | na                    | (32-40)     | 35                  | (33-40)     |
| TDS                      | 9                    | 10                   | (8-10)      | 9                     | (9-10)      | 10                  | (8-10)      |
| TAS                      | 8                    | 8                    | (8-9)       | 8                     | (8-8)       | 8                   | (8-9)       |
| TPS                      | 8                    | 9                    | (8-9)       | 8                     | (8-8)       | 9                   | (8-9)       |
| UGR                      | 10                   | 11                   | (10-12)     | 11                    | (10-11)     | 12                  | (10-12)     |
| LGR                      | 20                   | 20                   | (19-23)     | 20                    | (20-21)     | 21                  | (19-23)     |
| total GR                 | 30                   | 31                   | (30-35)     | na                    | (30-32)     | 31                  | (30-35)     |

**Diagnosis.** *Coregonus steinmanni* is a large whitefish with moderate pigmentation of all fins and body; light to dark greenish blue colour on the flanks above the lateral line; moderate to many pigmented small dots on the scales along the flank and the dorsum; deep bodied; stout caudal peduncle; short head; sub-terminal mouth; small eye with a thick and triangular shaped eye socket.

**Differential diagnosis.** *Coregonus steinmanni* occurs only in Lake Thun and we therefore compare the characters of this species specifically with the species of Lake Thun. Differential diagnoses against *C. albellus*, *C. alpinus*, and *C. fatioides* are given under those species' accounts.

#### *Coregonus steinmanni*-*Coregonus profundus*

*Coregonus steinmanni* can be distinguished from *C. profundus* by having more and longer gill rakers (upper arch gill raker number: 10–12, mode = 11 vs. 5–10, mode = 9; lower arch gill raker number: 19–23, mode = 20 vs. 10–18, mode = 14; total gill raker number: 30–35, mode = 31 vs. 15–27, mode = 21; middle gill raker length: 9.1–14.3% HL, mean = 11.5 vs. 7.6–11.7% HL, mean = 9.2; longest gill raker length: 10–14.4% HL, mean = 12.1 vs. 7.8–12.4% HL, mean = 10.1), shorter pectoral fin (pectoral fin 1 length: 13.9–18.2% SL, mean = 16.2 vs. 16.6–21% SL, mean = 18.4; pectoral fin 2 length: 15.2–19.1% SL, mean = 17 vs. 17.7–23.2% SL, mean = 20.2), a shorter head (13.2–15.1% SL, mean = 14 vs. 15.5–18.4% SL, mean = 16.4), a smaller eye cavity (24.2–27.8% HL, mean = 26.2 vs. 26.2–32.1% HL, mean = 29.2), a narrower underjaw (19.3–25, mean = 23% HL vs. 22.7–29.2% HL, mean = 26), and a shorter prepelvic distance (48.6–54.3% SL, mean = 51.7 vs. 51.2–58.1% SL,



**Figure 7.** *Coregonus steinmanni*, Lake Thun, Switzerland **A** holotype, NMBE-1077219, Lake Thun, 301 mm SL, female, freshly caught specimen **B, C** NMBE-1077219, holotype, preserved specimen **D** paratype, NMBE-1077214, Lake Thun, 234 mm SL, female, freshly caught specimen. The white scale (1cm) below each fish acts as a reference for the actual size of the specimen.

mean = 54.2). Based on ratios *C. steinmanni* can be differentiated from *C. profundus* by having a larger “caudal fin depth / dorsal head length” ratio (0.53–0.63 vs. 0.4–0.49) (Tables 6, 8, 10, Suppl. material 1: Table S6).

***Coregonus steinmanni*-*Coregonus acrinus***

*Coregonus steinmanni* differs from *C. acrinus* by having a shorter maxilla (18.1–21.8% HL, mean = 19.7 vs. 19.4–23.8% HL, mean = 21.8) (Tables 6, 8) and can be differentiated based on ratios from *C. acrinus* by having a larger “caudal peduncle depth / maxilla length” ratio (1.86–2.24 vs. 1.4–1.9) (Tables 6, 9, 10).

**Description.** General appearance is shown in Figure 7. Morphological and meristic characters of both sexes can be found in Table 6 and Suppl. material 1: Table S6 and first- and second-best ratios for both sexes combined can be found in Table 10. The description is valid for both sexes.

**Shape:** Generally deep bodied with greatest body depth anterior of the dorsal fin. Dorsal profile strongly arched compared to ventral profile. Dorsal profile from the tip of snout to the anterior origin of dorsal fin moderate to strongly convex, whereas the ventral profile is slightly arched such that it is almost straight or slightly convex from the interorbital area to the pelvic fin origin. Mouth is rather thin (i.e., width of upper and lower jaw), short and sub-terminal. Snout is pronounced and almost equally wide as deep resulting in an almost square shape. Small eye. Eye-socket is thick and triangular (i.e., sickle-shaped). Pectoral fin moderately tapered. The anterior unbranched ray of the erected dorsal fin has an approx. 60° angle to body axis and at the end of the ray it is bent posteriorly. Caudal peduncle is stout and short. Caudal fin forked and sometimes slightly asymmetrical with the dorsal part being longer. Un-branched ray of anal fin mostly straight and only sometimes slightly bent posteriorly. Anal fin longest anteriorly and progressively shortening posteriorly with the outer margin of the anal fin mostly slightly concave and only rarely straight.

**Meristics:** Few and short gill rakers.

**Colour:** Pigmentation of fins and body overall moderately strong in live specimens. Pectoral fin is moderately to strongly pigmented. Dorsal, adipose, pelvic, anal, and caudal fins are moderately to strongly pigmented. Silvery appearance along the flanks with moderate to many pigmented small dots on the scales. The dots are found along the flank and the dorsum. Distribution of the dots is bound to the scale patterning such that the dots are found at the edge of the scales or at the boundary point of two scales (as can be found for the species of *C. fatioi*, *C. alpinus* and *C. brienzi*). Dorsally above the lateral line the silvery appearance changes to a light (e.g., RGB (135, 236, 179)) or darker greenish blue colour (e.g., RGB (7,168,125)). Dorsal part of the head strongly pigmented. Snout around the nostrils strongly pigmented with a gap of moderate pigmentation posteriorly of the nostrils up to the height of the middle of the eyes. Pre-operculum and operculum are silvery with one black dot on the lower margin of the pre-operculum. For a comparison to the main colouration found in the other species see Suppl. material 1: Figure S8. Preserved specimens are pale in colouration with similar pigmentation as described for live specimens. Silvery, translucent, not coloured or unpigmented parts of the body become brown-yellowish (e.g., RGB (239, 210, 40)), whereas the pigmented parts are conserved and the coloured parts (dorsally above the lateral line) become brownish (e.g., RGB (186, 140, 100)).

**Distribution and notes on biology.** *Coregonus steinmanni* is found in Lake Thun (46°40'N, 7°46'E), which is connected to Lake Brienz through the river Aare at Interlaken. Based on isotopic signatures *C. steinmanni* feeds on a mix of benthic prey and zooplankton (Selz 2008; Hudson 2011; Ingram et al. 2012) and has a fast growth rate (Bittner 2009). It has to be noted that the work by Selz (2008), Hudson (2011) and Ingram et al. (2012) did not yet separate *C. alpinus* from *C. steinmanni*, which are phenotypically difficult to distinguish. Only recently has genetic work by Dönz and colleagues (2018) clearly resolved that these are two distinct species. Thus, the isotopic work by Selz (2008), Hudson (2011) and Ingram et al. (2012) most likely comprises of specimens of both species. The gill raker number of *C. steinmanni* (more gill rakers) and *C. alpinus* (fewer gill rakers) suggests – based on the functional properties of the number of gill rakers on feeding on different prey items (Lundsgaard-Hansen et al. 2013; Roesch et al. 2013) – that *C. steinmanni* feeds more on zooplankton and less on benthic prey than *C. alpinus*, but this assumption needs to be verified in the future with stomach content analyses. Interestingly, the relative species abundances in the pelagic and benthic habitat from a habitat stratified random sampling in Lake Thun (mid-October 2013: Vonlanthen et al. 2015) shows, that *C. steinmanni* is occupying the moderately deep waters of the benthic habitat (76 m;  $N = 1$ ) and the shallow waters of the pelagic habitat (8 m;  $N = 1$ ) (Dönz et al. 2018). *Coregonus alpinus* on the other hand can exclusively be found in shallow water in the benthic habitat (first 13 m;  $N = 1$ ) and is completely absent from the pelagic habitat in Lake Thun (Dönz et al. 2018). It is to note that the habitat-stratified random sampling data only covers a short period of time (one month in late summer) and it is thus not clear how the species are distributed spatially through the rest of the year.

*Coregonus steinmanni* resembles phenotypically *C. alpinus* and to some extent *C. acrinusus*. The average size (total length) at 3 years of age for specimens in this study is  $328 \pm 23$  mm (mean and standard deviation,  $N = 11$ ) (Suppl. material 1: Figures S4–S6). The average size at 3 years of age for the specimens of *C. steinmanni* from this study is similar to that for the years 2004–2005 ( $338.5 \pm 19$  mm,  $N = 8$ ) (Bittner et al. unpublished; Vonlanthen et al. unpublished). The size of 3-year-old specimens of *C. steinmanni* is similar to that of *C. alpinus*, larger than that of *C. acrinusus* and considerably larger than that of *C. albellus*, *C. fatioi* and *C. profundus* (Suppl. material 1: Figure S6). *Coregonus steinmanni* has a short spawning season in late December and only rarely can be found spawning in late autumn (Suppl. material 1: Figure S3; Dönz et al. 2018). *Coregonus steinmanni* spawns mostly in moderately shallow waters of 10 m down to approx. 120 m (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). The spawning season and depth of *C. steinmanni* overlaps largely with that of *C. acrinusus* and *C. alpinus* and partially with that of *C. fatioi*. To a much lesser extent the spawning depth and time of *C. steinmanni* also overlaps with that of *C. albellus* and *C. profundus*.

**Etymology.** The specific epithet *steinmanni* is the genitive of *Steinmann*. We name this species after the high school teacher and researcher Paul Steinmann, a zoologist from Switzerland who wrote the most comprehensive compendium on Swiss whitefish to date and compiled throughout his lifetime a large collection of preserved specimens

of Swiss, but also European, fishes (Steinmann 1950). This collection and his work on the revision of Swiss whitefish together with work by Fatio (1890) has been essential to describe the whitefish diversity that was present in Switzerland just before or at the beginning of the strong anthropogenic-induced eutrophication of many Swiss lakes which was accompanied by population collapse, speciation reversals, and extinction of Swiss whitefish (Vonlanthen et al. 2012). For example, the only existing specimens of a now-extinct whitefish species, *C. gutturosus* Gmelin 1818, can only be found in the collection of Paul Steinmann.

**Common name.** None; this species was not recognized by local fishermen or fisherwomen as distinct from *C. alpinus* and was thus also called “Balchen”. We suggest the German name “Steinmann’s Balchen”.

***C. brienzii* Selz, Dönz, Vonlanthen & Seehausen, sp. nov.**

<http://zoobank.org/C42663B8-4D34-4499-85D9-259AB7DA204B>

**Figure 8**

*Coregonus* “Felchen”: Kirchhofer 1990; Kirchhofer 1995 (see also synonymy of *C. alpinus* and *C. fatioi*)

*Coregonus* “Large type”: Maurer and Guthruf 2005; Müller et al. 2007 (see also synonymy of *C. fatioi* and *C. alpinus*)

*Coregonus* sp. “Balchen”: Hudson et al. 2011, 2013, 2016; Ingram et al. 2012; Vonlanthen et al. 2012, 2015; Vonlanthen and Périat 2013 (see also synonymy of *C. alpinus* and *C. steinmanni*)

*Coregonus* sp. “Balchen 2”: Dönz et al. 2018 (see also synonymy of *C. steinmanni*)

**Material examined. Holotype.** NMBE-1077126, Switzerland, Lake Brienz (46°43'N, 7°57'E), 223 mm SL, female.

**Paratypes.** NMBE-1077116–1077125, NMBE-1077127–1077128, Switzerland, Lake Brienz (46°43'N, 7°57'E), N = 12, 118–226 mm SL.

**Diagnosis.** *Coregonus brienzii* is a medium-sized whitefish with moderate pigmentation of all fins and body; light to dark greenish blue colour on the flanks above the lateral line; moderate to many pigmented small dots on the scales along the flank and the dorsum; deep bodied; stout caudal peduncle; short head; moderately large eye with a moderately thick and triangular shaped eye socket.

**Differential diagnosis.** *Coregonus brienzii* occurs only in Lake Brienz and we therefore compare the characters of this species specifically with the species of Lake Brienz. Differential diagnoses against *C. albellus*, *C. alpinus*, and *C. fatioi* are given under those species’ accounts.

**Description.** General appearance is shown in Figure 8. Morphological and meristic characters of both sexes can be found in Table 7 and Suppl. material 1: Table S6 and first- and second-best ratios for both sexes combined can be found in Table 11. The description is valid for both sexes.

**Table 7.** Morphological and meristic data of *C. brienzi* from Lake Brienz, Switzerland, NMBE-1077126, female, holotype; paratypes N = 12. For females and for both sexes the range and the mean include the holotype.

| Morphological characters             | <i>C. brienzi</i><br>Holotype | Lake Brienz          |               |                       |               |                     |               |
|--------------------------------------|-------------------------------|----------------------|---------------|-----------------------|---------------|---------------------|---------------|
|                                      |                               | Both sexes           |               |                       |               |                     |               |
|                                      |                               | <i>N</i> -total = 13 |               | <i>N</i> -females = 4 |               | <i>N</i> -males = 9 |               |
|                                      |                               | Mean ± Stdev         | Range         | Mean ± Stdev          | Range         | Mean ± Stdev        | Range         |
| SL (mm)                              | 223.0                         | 181.5±37.0           | (118–226)     | 187.8±47.4            | (118–223)     | 178.7±34.3          | (129–226)     |
| <b>Percentage of standard length</b> |                               |                      |               |                       |               |                     |               |
| PelvFB                               | 4.1                           | 3.7±0.6              | (2.8–4.8)     | 3.6±0.6               | (2.8–4.2)     | 3.8±0.6             | (2.9–4.8)     |
| PelvFS                               | 6.1                           | 6.1±0.8              | (4.6–7.4)     | 5.8±0.4               | (5.1–6.1)     | 6.3±0.9             | (4.6–7.4)     |
| PelvF                                | 15.2                          | 15.6±1.1             | (14–17.5)     | 15±0.5                | (14.6–15.7)   | 15.9±1.2            | (14–17.5)     |
| PecFB                                | 3.1                           | 3.1±0.2              | (2.6–3.4)     | 3.0±0.3               | (2.6–3.2)     | 3.1±0.2             | (2.8–3.4)     |
| PecF1                                | 16.0                          | 15.9±1.6             | (13.9–20.1)   | 15.4±0.7              | (14.5–16.0)   | 16.2±1.8            | (13.9–20.1)   |
| PecF2                                | 17.0                          | 16.8±1.6             | (14–20.7)     | 16.4±0.7              | (15.5–17)     | 17±1.9              | (14–20.7)     |
| DFB                                  | 12.3                          | 11.8±0.8             | (10.4–12.9)   | 11.7±0.4              | (11.3–12.3)   | 11.9±1.0            | (10.4–12.9)   |
| DFAc                                 | 17.6                          | 17.9±1.2             | (15.5–19.8)   | 17.7±0.7              | (16.9–18.6)   | 18.0±1.4            | (15.5–19.8)   |
| DFAd                                 | 18.7                          | 18.6±1.5             | (15.3–20.8)   | 18.3±0.4              | (17.8–18.7)   | 18.8±1.8            | (15.3–20.8)   |
| DFPe                                 | 5.1                           | 5.2±0.6              | (4.2–6.5)     | 5.0±0.2               | (4.7–5.2)     | 5.3±0.7             | (4.2–6.5)     |
| AFB                                  | 13.7                          | 12.4±0.9             | (11.1–13.7)   | 12.9±1.1              | (11.4–13.7)   | 12.2±0.7            | (11.1–13.6)   |
| AFAc                                 | 11.1                          | 11.2±1.0             | (9.4–12.6)    | 11.2±0.5              | (10.5–11.6)   | 11.2±1.2            | (9.4–12.6)    |
| AdFB                                 | 5.1                           | 5.5±0.8              | (4.0–7.1)     | 5.2±0.3               | (5.0–5.7)     | 5.6±0.9             | (4.0–7.1)     |
| CF                                   | 23.8                          | 24.1±1.1             | (22.6–26.3)   | 23.2±0.5              | (22.6–23.8)   | 24.5±1.1            | (22.7–26.3)   |
| CD                                   | 7.3                           | 7.3±0.3              | (6.7–7.7)     | 7.1±0.4               | (6.7–7.5)     | 7.4±0.2             | (7.1–7.7)     |
| CL                                   | 13.9                          | 13.8±1.0             | (12.2–15.8)   | 14.0±0.4              | (13.7–14.6)   | 13.7±1.1            | (12.2–15.8)   |
| PaDc                                 | 18.8                          | 19.1±0.7             | (17.9–20.7)   | 19±0.4                | (18.6–19.4)   | 19.1±0.9            | (17.9–20.7)   |
| DHL                                  | 15.0                          | 15.6±0.7             | (14.6–16.8)   | 15.4±0.6              | (15.0–16.3)   | 15.7±0.7            | (14.6–16.8)   |
| PreP                                 | 48.6                          | 51.1±1.7             | (47.8–54.0)   | 50.9±1.8              | (48.6–52.8)   | 51.2±1.8            | (47.8–54.0)   |
| PreA                                 | 75.3                          | 77.1±1.5             | (74.3–79.5)   | 76.2±1.7              | (74.3–78.2)   | 77.5±1.3            | (75.4–79.5)   |
| PreD                                 | 46.2                          | 47.5±1.7             | (43.9–49.4)   | 47.2±1.1              | (46.2–48.2)   | 47.6±2              | (43.9–49.4)   |
| BD                                   | 24.6                          | 22.6±1.7             | (19.6–25.1)   | 22.7±2.5              | (20.5–25.1)   | 22.6±1.5            | (19.6–24.2)   |
| PostD                                | 45.9                          | 44.1±1.1             | (42.4–45.9)   | 44.6±1.3              | (43–45.9)     | 43.9±1.1            | (42.4–45.5)   |
| TL                                   | 122.0                         | 121.5±1.9            | (117.8–124.4) | 121.2±2.5             | (117.8–123.8) | 121.6±1.7           | (119.2–124.4) |
| HL (mm)                              | 45.4                          | 38.7±7.3             | (26.7–47.4)   | 39.2±8.5              | (26.7–45.4)   | 38.5±7.3            | (28.3–47.4)   |
| <b>Percentage of head length</b>     |                               |                      |               |                       |               |                     |               |
| SN                                   | 25.6                          | 23.3±1.8             | (20.5–26.3)   | 23.6±2.1              | (21.1–25.6)   | 23.2±1.7            | (20.5–26.3)   |
| ED                                   | 24.4                          | 25.3±1.6             | (23.1–28.3)   | 25.2±1.6              | (24.2–27.6)   | 25.3±1.7            | (23.1–28.3)   |
| EC                                   | 27.8                          | 29±2.3               | (25.6–32.9)   | 28.8±3.1              | (25.6–32.9)   | 29.1±2.1            | (26.5–32.7)   |
| EH                                   | 22.0                          | 24.4±1.4             | (22–27.2)     | 23.9±1.7              | (22–26.2)     | 24.7±1.3            | (23–27.2)     |
| ES                                   | 3.5                           | 4.7±1.2              | (3.3–7.2)     | 4.8±1.4               | (3.5–6.5)     | 4.7±1.2             | (3.3–7.2)     |
| PostO                                | 50.9                          | 50.7±1.1             | (48.2–52.3)   | 49.8±1.5              | (48.2–51.1)   | 51.1±0.7            | (50.3–52.3)   |
| HD                                   | 75.2                          | 68.5±3.3             | (64.4–75.2)   | 69.8±4.4              | (65.2–75.2)   | 67.9±2.8            | (64.4–73.1)   |
| MW                                   | 9.7                           | 9.9±0.9              | (8.5–10.9)    | 9.4±0.8               | (8.5–10.3)    | 10.1±0.8            | (8.6–10.9)    |
| UJ                                   | 30.2                          | 29.5±1.6             | (27.1–32)     | 29±1.8                | (27.1–30.8)   | 29.6±1.6            | (27.3–32)     |
| LJ                                   | 42.9                          | 42.2±1.5             | (40.5–45.7)   | 43.2±1.7              | (42–45.7)     | 41.8±1.2            | (40.5–43.7)   |
| M                                    | 23.4                          | 21±2.4               | (15.4–24)     | 21±3.9                | (15.4–24)     | 21.1±1.7            | (18.3–23.8)   |
| SD                                   | 7.0                           | 8.8±1.4              | (6.4–11.6)    | 7.4±0.9               | (6.4–8.6)     | 9.4±1.2             | (8–11.6)      |
| SW                                   | 18.0                          | 17.8±1.2             | (15.7–20.2)   | 17.6±0.6              | (16.7–18)     | 17.8±1.4            | (15.7–20.2)   |
| HW                                   | 52.1                          | 48.1±3.1             | (44.1–52.4)   | 48.5±4                | (44.1–52.1)   | 47.9±2.9            | (44.1–52.4)   |
| IOW                                  | 28.4                          | 26.2±1.9             | (22.8–30.7)   | 26.3±1.7              | (25–28.4)     | 26.1±2.1            | (22.8–30.7)   |
| INW                                  | 9.7                           | 11.1±0.8             | (9.7–12.6)    | 10.8±0.7              | (9.7–11.2)    | 11.3±0.9            | (10–12.6)     |
| LJW                                  | 14.1                          | 11.5±1.2             | (10.1–14.1)   | 11.9±2                | (10.1–14.1)   | 11.3±0.6            | (10.5–12.4)   |
| UJW                                  | 25.9                          | 23.4±1.6             | (20.2–26.1)   | 23.3±2.3              | (20.2–25.9)   | 23.5±1.3            | (21.4–26.1)   |
| MGR                                  | 13.5                          | 13.5±1.3             | (10.9–15.1)   | 13.7±1.6              | (11.6–15.1)   | 13.3±1.3            | (10.9–14.9)   |
| LGR                                  | 13.9                          | 14.7±1.6             | (12.1–16.8)   | 14.8±2.2              | (12.1–16.8)   | 14.7±1.4            | (13–16.7)     |
| UA                                   | 20.4                          | 18.5±1.7             | (15.3–20.5)   | 19.6±0.8              | (18.5–20.4)   | 18±1.7              | (15.3–20.5)   |
| LA                                   | 40.4                          | 35.5±2               | (33–40.4)     | 37.2±2.5              | (35–40.4)     | 34.8±1.4            | (33–37.5)     |
| <b>Meristic characters</b>           |                               | <b>Mode</b>          | <b>Range</b>  | <b>Mode</b>           | <b>Range</b>  | <b>Mode</b>         | <b>Range</b>  |
| PelvF unbranched                     | 1                             | 1                    | (1–1)         | 1                     | (1–1)         | 1                   | (1–1)         |
| PelvF branched                       | 10                            | 10                   | (9–11)        | 10                    | (9–10)        | 10                  | (10–11)       |

| Meristic characters | <i>C. brienzi</i><br>Holotype | Lake Brienz          |         |                       |         |                     |         |
|---------------------|-------------------------------|----------------------|---------|-----------------------|---------|---------------------|---------|
|                     |                               | Both sexes           |         |                       |         |                     |         |
|                     |                               | <i>N</i> -total = 13 |         | <i>N</i> -females = 4 |         | <i>N</i> -males = 9 |         |
|                     |                               | Mode                 | Range   | Mode                  | Range   | Mode                | Range   |
| PecF unbranched     | 1                             | 1                    | (1–1)   | 1                     | (1–1)   | 1                   | (1–1)   |
| PecF branched       | 15                            | 15                   | (15–17) | 15                    | (15–17) | 15                  | (15–17) |
| DF unbranched       | 4                             | 4                    | (3–4)   | 4                     | (4–4)   | 4                   | (3–4)   |
| DF branched         | 12                            | 11                   | (10–13) | 11                    | (10–12) | 10                  | (10–13) |
| AF unbranched       | 4                             | 4                    | (3–4)   | 4                     | (4–4)   | 4                   | (3–4)   |
| AF branched         | 13                            | 12                   | (11–13) | 13                    | (11–13) | 12                  | (12–12) |
| LS                  | 89                            | 86                   | (80–91) | 89                    | (80–91) | 86                  | (80–88) |
| PDS                 | 36                            | 35                   | (32–40) | na                    | (34–37) | 32                  | (32–40) |
| TDS                 | 9                             | 9                    | (7–10)  | 9                     | (7–9)   | 9                   | (8–10)  |
| TAS                 | 8                             | 8                    | (7–8)   | 8                     | (7–8)   | 8                   | (7–8)   |
| TPS                 | 8                             | 8                    | (8–9)   | 8                     | (8–8)   | 8                   | (8–9)   |
| UGR                 | 14                            | 14                   | (11–14) | 13                    | (13–14) | 12                  | (11–14) |
| LGR                 | 25                            | 24                   | (20–25) | 24                    | (24–25) | 23                  | (20–25) |
| total GR            | 39                            | 37                   | (32–39) | 37                    | (37–39) | 32                  | (32–38) |

**Shape:** Moderately deep bodied with greatest body depth anterior of the dorsal fin. Dorsal profile moderately arched compared to ventral profile. The dorsal profile from the tip of snout to the anterior origin of dorsal fin is moderately convex, whereas the ventral profile is slightly arched such that is almost straight or slightly convex from the interorbital area to the pelvic fin origin. In some specimens the ventral profile and dorsal profile are similar and only slightly arched. Head moderately short. Mouth is rather thin (i.e., width of upper and lower jaw), moderately short and terminal to sub-terminal. The snout can range from almost equally wide as deep to wider than deep, and is only moderately pronounced, since the tip of the snout can sometimes be fleshy and roundish. Moderately large eye. The eye-socket is thick and triangular (i.e., sickle-shaped). Pectoral fin moderately tapered. The anterior unbranched ray of the erected dorsal fin is almost vertically straight with an approx. 70–80° angle to the body axis and is only bent slightly posteriorly at the end of the ray. Caudal peduncle is moderately stout and short. Caudal fin forked and sometimes slightly asymmetrical with the dorsal part being longer. Unbranched ray of anal fin mostly straight and only sometimes slightly bent posteriorly. Anal fin longest anteriorly and progressively shortening posteriorly with the outer margin of the anal fin mostly slightly concave and only rarely straight.

**Meristics:** Many gill rakers that are moderately long.

**Colour:** Pigmentation of fins and body overall moderate in live specimens. The pectoral fin is mostly translucent and only rarely moderately pigmented at the median to distal parts of the fin. The dorsal, adipose, pelvic, anal, and caudal fins are moderately pigmented. Silvery appearance along the flanks with moderate to many pigmented small dots on the scales. The dots are found along the flank and the dorsum. The distribution of the dots is bound to the scale patterning such that the dots are found at the edge of the scales or at the boundary point of two scales (as can be found for the species of *C. alpinus* and *C. fatioi* from both lakes and *C. steinmanni* from Lake Thun). Dorsally above the lateral line the silvery appearance changes to a light (e.g., RGB (135, 236, 179)) or darker greenish blue colour (e.g., RGB (7,168,125)). The dorsal part of the head is moderately pigmented. The snout around the nostrils is



**Figure 8.** *Coregonus brienzi*, Switzerland, Lake Brienz **A** holotype, NMBE-1077126, 223 mm SL, female, freshly caught specimen **B, C** holotype, NMBE-1077126, preserved specimen **D** paratype, NMBE-1077116, 210.5 mm SL, female.

moderately pigmented with a gap of very weak pigmentation posteriorly of the nostrils up to the height of the middle of the eyes. The pre-operculum and operculum are silvery with one black dot on the lower margin of the pre-operculum. For a comparison

to the main colouration found in the other species see Suppl. material 1: Figure S8. Preserved specimens are pale in colouration with similar pigmentation as described for live specimens. The silvery, translucent, not coloured or unpigmented parts of the body become brown-yellowish (e.g., RGB (239, 210, 40)), whereas the pigmented parts are conserved and the coloured parts (dorsally above the lateral line) become brownish (e.g., RGB (186, 140, 100)).

**Distribution and notes on biology.** *Coregonus brienzi* is found in Lake Brienz (46°43'N, 7°57'E) which is connected with Lake Thun through the river Aare at Inter-laken. Our previous genetic work (DöNZ et al. 2018) suggested that *C. brienzi* is the same species as *C. steinmanni* and that it together with the other three species, *C. alpinus*, *C. fatioi*, and *C. albellus*, is present in both lakes. All four species displayed the same genetic relationships in both lakes (i.e., the same hierarchical grouping into distinct genotypic clusters and similar extends of genetic divergence). However, recent analyses of whole-genome data (De-Kayne et al. unpublished) revealed, that specimens of *C. steinmanni* from Lake Thun do not group with those of *C. brienzi*, whereas those of the other three species from both lakes do cluster together. Instead the whole genome data suggests that *C. steinmanni* clusters closer to *C. alpinus* from Lake Thun – as has previously been shown with genetic data (DöNZ et al. 2018) – and that *C. brienzi* clusters closer to *C. fatioi* from Lake Brienz. Interestingly, we also find morphological relationships to differ between the lakes; in Lake Thun *C. steinmanni* groups in morphospace with *C. alpinus*, whereas in Lake Brienz *C. brienzi* groups in morphospace with *C. fatioi*.

*Coregonus brienzi* most likely feeds on a mix of benthic prey and zooplankton (stomach content: Maurer and Guthruf 2005; Müller et al. 2007; isotopic signatures: Selz 2008; Hudson 2011) and has a moderately fast growth rate (Müller et al. 2007). It has to be noted that the work by Kirchhofer (1995), Maurer and Guthruf (2005) and Müller et al. (2007) did not distinguish between all species in Lake Brienz and thus lumped different species together into few groups. Maurer and Guthruf (2005) and Müller et al. (2007) differentiated between “small-type” and “large-type” whitefish based on cohort-specific threshold values for length-at age. Based on morphology and ecology Kirchhofer (1995) differentiated in Lake Brienz between “Felchen” (comprising most likely of *C. alpinus*, *C. fatioi* and *C. brienzi*) and “Brienzig” and “Winter-Brienzig” (comprising of summer- and winter-spawning specimens of *C. albellus*). Also, the isotopic work by Selz (2008), and Hudson (2011) did not yet differentiate between *C. fatioi* and *C. brienzi*. The relative species abundances in the pelagic and benthic habitat from a habitat-stratified random sampling of Lake Brienz (mid-September 2011: Vonlanthen et al. 2013) shows, that *C. brienzi* is absent from the benthic habitat and is present in the moderately deep pelagic waters (30 m;  $N = 1$ ) (DöNZ et al. 2018). It is to note that the habitat-stratified random sampling data only covers a short period of time (one month in late summer) and it is thus not clear how the species is distributed spatially through the rest of the year. *Coregonus brienzi* resembles phenotypically *C. fatioi*. The average size (total length) at 3 years of age for specimens in this study is  $254 \pm 14$  mm ( $N = 8$ ) (Suppl. material 1: Figures S5, S6). The size at 3 years of age of *C. brienzi* is similar to that of *C. fatioi*, slightly smaller than that of *C. alpinus* and consider-

ably larger than that of *C. albellus* (Suppl. material 1: Figure S6). *Coregonus brienzi* has a short spawning season in late December (Suppl. material 1: Figure S3; Dönz et al. 2018). *Coregonus brienzi* spawns mostly in moderately shallow waters of 10 m down to 60 m and rarely to 100 m (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). The spawning season and depth of *C. brienzi* overlaps largely with that *C. fatioi*.

**Etymology.** The specific epithet *brienzi* is the genitive of *Brienz*. We name this species after Lake Brienz, as it is the only endemic whitefish species known for Lake Brienz.

**Common name.** None. We suggest the German name «Brienzer Kleinbalchen»

***Coregonus profundus* Selz, Dönz, Vonlanthen & Seehausen, sp. nov.**

<http://zoobank.org/6B17CFFD-08A3-4A6E-A4AA-CAE0678370FF>

**Figure 9**

*Coregonus alpinus*: Kottelat 1997; Kottelat and Freyhof 2007; Hudson et al. 2011, 2013, 2016; Ingram et al. 2012; Vonlanthen et al. 2012, 2015; Dönz et al. 2018

*Coregonus lavaretus* natio *arurensis*, oekot. *profundus*: Steinmann 1950

*Coregonus* "Tiefenalbock", "Kropfer": Steinmann 1950

*Coregonus* "Kropfer": Heuscher 1901

*Coregonus* "Kropfer": Ruffi 1978, 1979; Kirchhofer and Tschumi 1986; Kirchhofer 1995; Bittner et al. 2010 (see also synonymy of *C. albellus*)

*Coregonus* "Kropfer", "THU3": Douglas et al. 1999, 2003; Douglas and Brunner 2002

**Material examined. Holotype.** NMBE-1077208, Switzerland, Lake Thun (46°40'N, 7°46'E), 194 mm SL, male.

**Paratypes.** NMBE-1077161–1077179, NMBE-1077203–1077207, NMBE-1077209–1077211, Switzerland, Lake Thun (46°40'N, 7°46'E), N = 27, 188–316 mm SL.

**Diagnosis.** *Coregonus profundus* is a small whitefish species with moderate pigmentation of all fins and the body; brown-orange colouration on the flanks above the lateral line; elongate slender body; long head; large eye with a thick and triangular shaped eye socket; tip of snout is fleshy and roundish; few (15–27) and short gill rakers.

**Differential diagnosis.** *Coregonus profundus* occurs only in Lake Thun and we therefore compare the characters of this species specifically with the species of Lake Thun. The differential diagnoses against *C. albellus*, *C. alpinus*, *C. fatioi*, and *C. steinmanni* are given under those species' accounts. The lower number of gill rakers of *C. profundus* (total gill raker number: 15–27, mode = 21) distinguishes this species from all other 5 whitefish species, *C. albellus* (32–44, mode = 38), *C. alpinus* (25–34, mode = 30), *C. fatioi* (32–43, mode = 38), *C. steinmanni* (30–35, mode = 31), and *C. acrinus* (30–40, mode = 36) (Suppl. material 1: Table S6).

***Coregonus profundus*–*Coregonus acrinus***

*Coregonus profundus* can be distinguished from *C. acrinus* by having shorter gill rakers (middle gill raker length: 7.6–11.7% HL, mean = 9.2 vs. 9.1–16.6% HL,

**Table 8.** Morphological and meristic data of *C. profundus* from Lake Thun, NMBE-1077208, male, holotype; paratypes N = 27. For ranges of males and for both sexes, the total range and mean include the holotype.

| Morphological characters             | <i>C. profundus</i><br>Holotype | Lake Thun            |               |                       |               |                      |               |
|--------------------------------------|---------------------------------|----------------------|---------------|-----------------------|---------------|----------------------|---------------|
|                                      |                                 | Both sexes           |               |                       |               |                      |               |
|                                      |                                 | <i>N</i> -total = 28 |               | <i>N</i> -females = 6 |               | <i>N</i> -males = 22 |               |
|                                      |                                 | Mean ± Stdev         | Range         | Mean ± Stdev          | Range         | Mean ± Stdev         | Range         |
| SL (mm)                              | 194.0                           | 223.3±26.7           | (188–316)     | 248.7±42.2            | (188–316)     | 216.3±16             | (188–241)     |
| <b>Percentage of standard length</b> |                                 |                      |               |                       |               |                      |               |
| PelvFB                               | 4.4                             | 4.2±0.3              | (3.6–5.0)     | 4.2±0.2               | (4–4.5)       | 4.2±0.4              | (3.6–5)       |
| PelvFS                               | 7.2                             | 6.0±0.8              | (4.0–7.2)     | 5.7±1                 | (4–6.8)       | 6.1±0.7              | (4.8–7.2)     |
| PelvF                                | 16.9                            | 17.7±1.1             | (15.1–19.6)   | 17.3±0.9              | (16.5–18.9)   | 17.9±1.1             | (15.1–19.6)   |
| PecFB                                | 3.5                             | 3.7±0.2              | (3.2–4.3)     | 3.6±0.2               | (3.2–3.8)     | 3.7±0.2              | (3.4–4.3)     |
| PecF1                                | 16.9                            | 18.4±1.1             | (16.6–21.0)   | 18.1±1.3              | (16.6–19.8)   | 18.5±1               | (16.8–21)     |
| PecF2                                | 17.8                            | 20.2±1.3             | (17.7–23.2)   | 19.9±1.5              | (17.7–22.1)   | 20.2±1.3             | (17.8–23.2)   |
| DFB                                  | 12.6                            | 12.5±0.9             | (10.5–14.5)   | 12.3±0.7              | (11.3–13.4)   | 12.5±1               | (10.5–14.5)   |
| DFAe                                 | 18.7                            | 19.5±1.4             | (15.9–21.9)   | 18.7±1.9              | (15.9–21.6)   | 19.7±1.2             | (17–21.9)     |
| DFAd                                 | 20.6                            | 20.7±1.3             | (17.5–23.2)   | 19.9±1.4              | (17.5–21.5)   | 20.9±1.2             | (18.3–23.2)   |
| DFPe                                 | 5.1                             | 5.0±0.5              | (3.9–6.1)     | 5.1±0.4               | (4.5–5.6)     | 5±0.6                | (3.9–6.1)     |
| AFB                                  | 13.5                            | 13.2±1.0             | (10.8–15.3)   | 13.4±0.8              | (12.1–14.4)   | 13.1±1.1             | (10.8–15.3)   |
| AFAe                                 | 13.6                            | 13.3±1.0             | (10.9–14.7)   | 12.8±1                | (10.9–13.9)   | 13.4±0.9             | (11.3–14.7)   |
| AdFB                                 | 5.1                             | 5.3±0.6              | (3.8–6.3)     | 5.3±0.4               | (4.6–5.8)     | 5.2±0.6              | (3.8–6.3)     |
| CF                                   | 24.1                            | 24.5±1.4             | (21.8–27.8)   | 24.3±2                | (21.8–27.8)   | 24.6±1.3             | (22.2–27.8)   |
| CD                                   | 7.5                             | 7.3±0.3              | (6.5–7.9)     | 7.5±0.2               | (7.2–7.8)     | 7.3±0.3              | (6.5–7.9)     |
| CL                                   | 12.5                            | 11.8±0.7             | (10.2–13.0)   | 12±0.8                | (10.9–13)     | 11.8±0.7             | (10.2–13)     |
| PaDc                                 | 16.9                            | 18.3±1.1             | (15.8–20.1)   | 18.5±0.9              | (17.1–19.6)   | 18.2±1.1             | (15.8–20.1)   |
| DHL                                  | 16.4                            | 16.4±0.6             | (15.5–18.4)   | 16.2±0.5              | (15.5–16.7)   | 16.5±0.6             | (15.7–18.4)   |
| PreP                                 | 55.2                            | 54.2±1.5             | (51.2–58.1)   | 53.3±1.2              | (51.2–54.1)   | 54.5±1.4             | (52.1–58.1)   |
| PreA                                 | 79.2                            | 78.4±1.4             | (75.0–80.6)   | 77.8±1.3              | (75.8–79.4)   | 78.6±1.4             | (75–80.6)     |
| PreD                                 | 48.5                            | 48.3±1.3             | (45.8–51.1)   | 47.8±1.8              | (45.8–50)     | 48.5±1.2             | (46.9–51.1)   |
| BD                                   | 24.4                            | 24.2±1.4             | (22.1–27.6)   | 25.4±1.3              | (24–27.6)     | 23.9±1.2             | (22.1–26.6)   |
| PostD                                | 40.6                            | 42.5±1.5             | (38.9–44.5)   | 43.2±1.4              | (41.3–44.5)   | 42.3±1.5             | (38.9–44.4)   |
| TL                                   | 122.2                           | 121.3±1.7            | (117.3–125.6) | 120.5±1.1             | (118.9–121.8) | 121.5±1.8            | (117.3–125.6) |
| HL (mm)                              | 41.2                            | 48.9±5.5             | (39.8–66.2)   | 54.1±8.7              | (39.8–66.2)   | 47.4±3.2             | (41.2–53.7)   |
| <b>Percentage of head length</b>     |                                 |                      |               |                       |               |                      |               |
| SN                                   | 23.6                            | 23.5±0.8             | (21.8–24.8)   | 23.3±0.6              | (22.5–24)     | 23.6±0.8             | (21.8–24.8)   |
| ED                                   | 23.3                            | 23.8±1.4             | (21.3–26.2)   | 23.7±1.5              | (21.9–25.7)   | 23.8±1.4             | (21.3–26.2)   |
| EC                                   | 30.9                            | 29.2±1.4             | (26.2–32.1)   | 28.2±1.6              | (26.2–31.1)   | 29.5±1.3             | (26.9–32.1)   |
| EH                                   | 24.5                            | 23.6±0.9             | (21.8–25.5)   | 23.2±0.7              | (21.9–23.9)   | 23.7±0.9             | (21.8–25.5)   |
| ES                                   | 5.7                             | 4.6±0.8              | (3.0–5.9)     | 4.3±0.9               | (3.5–5.9)     | 4.7±0.7              | (3–5.7)       |
| PostO                                | 51.1                            | 50.9±1.4             | (48–54)       | 52.2±1.8              | (49.2–54)     | 50.6±1               | (48–52.1)     |
| HD                                   | 78.3                            | 71.8±2.8             | (65.9–78.3)   | 73±2.1                | (69.4–75.7)   | 71.5±2.9             | (65.9–78.3)   |
| MW                                   | 11.2                            | 10±0.8               | (8.5–11.7)    | 10±0.5                | (9.4–10.7)    | 10±0.9               | (8.5–11.7)    |
| UJ                                   | 29.1                            | 28.7±1.2             | (26.4–30.6)   | 28.1±1.3              | (26.4–30)     | 28.9±1.1             | (26.8–30.6)   |
| LJ                                   | 41.4                            | 39.9±1.7             | (37–43.6)     | 39.1±1.4              | (37–40.9)     | 40.1±1.8             | (37.2–43.6)   |
| M                                    | 24                              | 20.7±1.2             | (17.3–24)     | 20.1±1.4              | (17.3–21.2)   | 20.8±1.1             | (18.7–24)     |
| SD                                   | 10.1                            | 10±0.8               | (8.1–11.3)    | 9.7±0.6               | (8.8–10.7)    | 10±0.8               | (8.1–11.3)    |
| SW                                   | 17.6                            | 15.8±1.3             | (12.5–17.8)   | 15.3±1.6              | (13.7–17.3)   | 16±1.1               | (12.5–17.8)   |
| HW                                   | 57.3                            | 52.4±3.3             | (46.7–58.6)   | 53.1±3.9              | (46.7–58.6)   | 52.2±3.1             | (47.4–57.7)   |
| IOW                                  | 28.7                            | 28.1±1.2             | (26.1–30.3)   | 28.9±1.4              | (26.5–30.3)   | 27.9±1.1             | (26.1–29.5)   |
| INW                                  | 11.1                            | 11.1±1               | (8.2–13.3)    | 11.7±1.1              | (10.3–13.3)   | 10.9±1               | (8.2–12.5)    |
| LJW                                  | 9.3                             | 11.7±2.2             | (7.8–16.2)    | 12.7±0.7              | (11.4–13.6)   | 11.5±2.4             | (7.8–16.2)    |
| UJW                                  | 28.9                            | 26±1.7               | (22.7–29.2)   | 25.2±1.5              | (22.7–27.4)   | 26.2±1.7             | (22.8–29.2)   |
| MGR                                  | 10                              | 9.2±1.1              | (7.6–11.7)    | 9.4±1.2               | (7.6–10.9)    | 9.2±1.1              | (8–11.7)      |
| LGR                                  | 10.7                            | 10.1±1.2             | (7.8–12.4)    | 10.5±1.6              | (7.8–12.4)    | 9.9±1.1              | (8.1–12.3)    |
| UA                                   | 19.6                            | 18±1.8               | (15.5–21.8)   | 18.7±2.4              | (15.5–21.8)   | 17.8±1.6             | (15.5–21.2)   |
| LA                                   | 35.8                            | 34.3±1.8             | (30.3–37.7)   | 35.1±2.1              | (32.9–37.7)   | 34.1±1.7             | (30.3–36.6)   |
| <b>Meristic characters</b>           |                                 | <b>Mode</b>          | <b>Range</b>  |                       |               |                      |               |
| PelvF unbranched                     | 1                               | 1                    | (1–1)         | 1                     | (1–1)         | 1                    | (1–1)         |
| PelvF branched                       | 10                              | 10                   | (9–11)        | 10                    | (10–11)       | 10                   | (9–11)        |
| PecF unbranched                      | 1                               | 1                    | (1–1)         | 1                     | (1–1)         | 1                    | (1–1)         |

| Meristic characters | <i>C. profundus</i><br>Holotype | Lake Thun            |         |                       |         |                      |         |
|---------------------|---------------------------------|----------------------|---------|-----------------------|---------|----------------------|---------|
|                     |                                 | Both sexes           |         |                       |         |                      |         |
|                     |                                 | <i>N</i> -total = 28 |         | <i>N</i> -females = 6 |         | <i>N</i> -males = 22 |         |
|                     |                                 | Mode                 | Range   | Mode                  | Range   | Mode                 | Range   |
| PecF branched       | 16                              | 16                   | (13–17) | 16                    | (16–16) | 16                   | (13–17) |
| DF unbranched       | 5                               | 4                    | (3–5)   | 4                     | (3–4)   | 4                    | (3–5)   |
| DF branched         | 10                              | 10                   | (9–12)  | 11                    | (10–12) | 10                   | (9–11)  |
| AF unbranched       | 5                               | 3                    | (2–5)   | 2                     | (2–4)   | 3                    | (2–5)   |
| AF branched         | 11                              | 12                   | (11–14) | 12                    | (12–14) | 12                   | (11–13) |
| LS                  | 83                              | 84                   | (76–90) | 83                    | (80–89) | 84                   | (76–90) |
| PDS                 | 34                              | 34                   | (32–38) | 32                    | (32–37) | 34                   | (32–38) |
| TDS                 | 9                               | 9                    | (8–10)  | 9                     | (8–10)  | 9                    | (8–10)  |
| TAS                 | 8                               | 8                    | (6–8)   | 8                     | (8–8)   | 8                    | (6–8)   |
| TPS                 | 8                               | 8                    | (7–9)   | 9                     | (8–9)   | 8                    | (7–9)   |
| UGR                 | 8                               | 9                    | (5–10)  | 7                     | (6–10)  | 9                    | (5–9)   |
| LG R                | 13                              | 14                   | (10–18) | 17                    | (11–18) | 14                   | (10–18) |
| total GR            | 21                              | 21                   | (15–27) | na                    | (18–27) | 21                   | (15–26) |

mean = 13.4; longest gill raker length: 7.8–12.4% HL, mean = 10.1 vs. 11.4–16.9% HL, mean = 14.5) and a longer head (15.5–18.4% HL, mean = 16.4 vs. 13.8–16.1% HL, mean = 15.2) (Tables 8, 9).

**Description.** General appearance is shown in Figure 9. Morphological and meristic characters of both sexes can be found in Table 8 and Suppl. material 1: Table S6 and first- and second-best ratios for both sexes combined can be found in Table 10. The description is valid for both sexes.

**Shape:** Body elongate. Slender bodied with greatest body depth anterior of the dorsal fin. Dorsal and ventral profile similar and slightly arched. Dorsal and ventral profile from tip of snout to interorbital area mostly straight and then slightly convex to dorsal and pelvic fin origin respectively. Head long. Snout often 60° angle to the body axis anterior of the eye, such that the profile from the tip of the snout to the vertical projection where the anterior part of the eye crosses the dorsal profile is straight and afterwards slightly convex. Mouth is wide (i.e., width of upper and lower jaw), rather short and mostly strongly sub-terminal and only rarely terminal. Snout is weakly pronounced, since the tip of the snout is often fleshy and roundish. Eye rather large with a large eye cavity and a thick and triangular eye-socket (i.e., sickle-shaped). Pectoral fin long and moderately tapered. Dorsal fin long with the anterior unbranched ray of the erected dorsal fin approx. 70–80° angle to body axis and only slightly bent posteriorly at the end of the ray. Caudal peduncle narrow and short with caudal fin forked and sometimes moderately to strongly asymmetrical with either the ventral or dorsal part being longer. Unbranched ray of anal fin straight and rarely bent posteriorly at the end of the ray. Anal fin is longest anteriorly and progressively shortening posteriorly with the outer margin of the anal fin slightly concave and only rarely straight.

**Meristics:** Very few and very short gill rakers.

**Colour:** Pigmentation of fins and body is overall moderate in live specimens. Pectoral fin is translucent or yellowish in colouration with moderate pigmentation at the median to distal parts of the fin. Dorsal, adipose, pelvic, anal and caudal fins are moderately pigmented. Silvery appearance along the flanks and dorsally above the lateral line the silvery appearance changes to a pale brown-orange colouration (e.g., RGB



**Figure 9.** *Coregonus profundus*, Lake Thun, Switzerland **A** holotype, NMBE-1077208, Lake Thun, 194 mm SL, male, freshly caught specimen **B**, **C** holotype, NMBE-1077208, preserved specimen **D** paratype, NMBE-1077203, Lake Thun, 315.5 mm SL, male **E** paratype, NMBE-1077166, Lake Thun, 253.5 mm SL, female. The white scale (1 cm) below each fish acts as a reference for the actual size of the specimen.

(232, 172, 52)) and very rarely the brown-orange colouration can have a hint of light greenish colour (e.g., RGB (136, 245, 205)). Sometimes the colouration above the lateral line is pale rose (e.g., RGB (247, 187, 175)) and then towards the dorsum becomes a brown-orange. This transition from one colouration to another can also be observed in *C. albellus*. For a comparison to the main colouration found in the other species see Suppl. material 1: Figure S8. Dorsal part of the head is moderately pigmented. Snout around the nostrils is moderately pigmented and rarely with a gap of less pigmentation posteriorly of the nostrils up to the height of the middle of the eyes. The operculum and pre-operculum are silvery with one black dot on the lower margin of the pre-operculum. Preserved specimens are pale in colouration with similar pigmentation as described for live specimens. Silvery, translucent, not coloured or unpigmented parts of the body become brown-yellowish (e.g., RGB (239, 210, 40)), whereas the pigmented parts are conserved and the coloured parts (dorsally above the lateral line) become brownish (e.g., RGB (186, 140, 100)).

**Distribution and notes on biology.** *Coregonus profundus* is found in Lake Thun (46°40'N, 7°46'E). It is believed to have been endemic to this lake. Yet, based on matching genetic (microsatellite) and morphological (gill raker number, morphological characters) evidence one ripe specimen of *C. profundus* has been caught by a local fisherman, Stefan Dasen, in 2016 in Lake Biel (47°05'N, 7°10'E) (Suppl. material 1: Figure S9). Lake Biel has been artificially connected with Lake Thun through the river Aare since the Jura water correction from 1868–1878, where the river Aare was artificially bypassed downstream from Lake Thun into Lake Biel. For another Lake Thun species, *C. albellus*, it had been known since at least 2004 that it can be found in Lake Biel (see details in the note on biology for *C. albellus*) (Bittner 2009; this study Suppl. material 1: Figure S9).

It is important to note that native whitefish species of Lake Biel were only known to spawn in the winter months (Fatio 1885; Steinmann 1950; Ruffli 1978), whereas *C. profundus* as well as *C. albellus* spawn in late summer and winter. Our study reports the first record of *C. profundus* in Lake Biel. It is unclear though if *C. profundus* has established as a self-sustaining population in Lake Biel. So far, we only know of one ripe specimen of *C. profundus* from Lake Biel, whereas for *C. albellus* reasonable numbers of ripe specimens have been caught for several years in Lake Biel during what is the normal spawning period (late summer) of this species in lakes Thun and Brienz (Bittner 2009; 2016; Suppl. material 1: Figure S9). Based on isotopic signatures *C. profundus* feeds on benthic prey items (Selz 2008; Hudson 2011; Ingram et al. 2012) and has a slow growth rate (Bittner et al. unpublished). Interestingly specimens of *C. profundus* that have been caught on the spawning grounds of *C. albellus* were often in past-spawning condition and occasional stomach content analysis revealed that these fish had been heavily preying on whitefish eggs (Bittner 2009). Earlier stomach content analysis of *C. profundus* from the months of October and February of 1971 and 1972, respectively, showed that *C. profundus* mainly feed on chironomid larvae and occasionally on fish eggs (Ruffli 1979). Even earlier stomach content analysis by Steinmann (1950) also show that they feed on chironomid larvae, but also on pisidium and other benthic invertebrates. Habitat-stratified random sampling of Lake Thun (mid-October 2013:

Vonlanthen et al. 2015) shows that *C. profundus* occupies mostly the moderately deep to the deepest waters in the benthic habitat (approx. 15 – 210 m;  $N = 16$ ) and rarely the moderately deep pelagic waters (approx. 15 – 45 m;  $N = 3$ ) (Dönz et al. 2018). The habitat-stratified random sampling did not distinguish between ripe and unripe specimens, and thus in the case of *C. profundus*, the distribution pattern along the depth in the benthic zone is biased by the spawning aggregation of this species since the sampling period coincides partially with the spawning season of this species. *Coregonus profundus* phenotypically resembles superficially *C. albellus*. The average size (total length) at 3 years of age for specimens used in this study is  $263 \pm 16$  mm (mean and standard deviation,  $N = 11$ ) (Suppl. material 1: Figures S4, S6). The size of 3-year-old specimens of *C. profundus* is similar to that of *C. albellus* and *C. fatioi*, but smaller than that of *C. acrinus* and considerably smaller than that of *C. alpinus* and *C. steinmanni* (Suppl. material 1: Figure S6). *Coregonus profundus* has a moderately long spawning season from August to December with one major peak from late August to late September / early October (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). Spawning depth varies with spawning season and can range from approx. 30 m to 150 m (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). The spawning season and depth of *C. profundus* partially overlaps with that of *C. steinmanni*, *C. fatioi*, and *C. albellus* (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018).

*Coregonus profundus* is known by the common name “Kropfer” and has previously been described under the name *C. alpinus* (Kottelat (1997) and Kottelat and Freyhof (2007)). As we explain in detail under the species account of *C. alpinus*, the designated lectotype of *C. alpinus* is incongruent with the description of the species (with the common name “Kropfer”: Kottelat (1997) and Kottelat and Freyhof (2007)). We have thus retained the name *C. alpinus* for the lectotype designated by Kottelat (1997) and provided a new description of this taxon. For the species otherwise described by Kottelat (1997) and Kottelat and Freyhof (2007) as *C. alpinus* (with the common name “Kropfer”) we designated a new name, *C. profundus*.

**Etymology.** The adjective *profundus* means deep in Latin and is used for *C. profundus* to describe the species unique ecology of living and breeding in great depths in Lake Thun.

**Common name.** Kropfer.

***Coregonus acrinus* Selz, Dönz, Vonlanthen & Seehausen, sp. nov.**

<http://zoobank.org/FEB8CAC5-E55D-4A8C-8E21-94E4DB0E77B2>

**Figure 10**

*Coregonus* “Albock”: Kirchhofer 1995 (see also synonymy of *C. alpinus* and *C. steinmanni*)

*Coregonus* “Albock”, “THU1”: Douglas et al. 1999; Douglas and Brunner 2002; Douglas et al. 2003 (see also synonymy of *C. fatioi*)

*Coregonus fatioi*: Hudson et al. 2011, 2013, 2016; Ingram et al. 2012; Vonlanthen et al. 2012

*Coregonus* sp. “Albock”: Dönz et al. 2018

**Material examined. Holotype.** NMBE-1077271, Switzerland, Lake Thun (46°40'N, 7°46'E), 239.5 mm SL, male.

**Paratypes.** NMBE-1077238–1077240, NMBE-1077268–1077270, NMBE-1077272–1077290, Switzerland, Lake Thun (46°40'N, 7°46'E), N = 25, 197–278 mm SL.

**Diagnosis.** *Coregonus acrinus* is a medium-sized whitefish with moderate pigmentation of all fins and body; dark greenish blue colour on the flanks above the lateral line; moderate to many pigmented small dots on the scales; tip of the snout pointy; long head; small eye with a thick and triangular shaped eye socket; many and moderately long gill rakers.

**Differential diagnosis.** *Coregonus acrinus* only occurs in Lake Thun and shows ancestry contributions from whitefish of Lake Constance, besides its Lake Thun ancestry. These derive from historically documented introductions of at least two whitefish species (*C. wartmanni* and *C. macrophthalmus*) into Lake Thun. Since, historically undocumented introductions of other whitefish from Lake Constance cannot be excluded and since there is no clear genetic assignment of *C. wartmanni* or *C. macrophthalmus* as likely source of the allochthonous introgression we compare the characters of this species with those of all whitefish species from Lake Constance and all other whitefish species from Lake Thun. The differential diagnoses against *C. albellus*, *C. alpinus*, *C. fatioi*, *C. steinmanni* and *C. profundus* are given under those species' accounts.

#### **Lake Constance comparison.**

##### ***Coregonus acrinus*—all four Lake Constance species**

The wider underjaw of *C. acrinus* (9.2–14.3% HL, mean = 12.2) differentiates it from all other species from Lake Constance, *C. gutturosus* (6.8–9.9% HL, mean = 7.7), *C. arenicolus* (7.8–8.5% HL, mean = 8.1), *C. macrophthalmus* (6.4–8.8% HL, mean = 8) and *C. wartmanni* (8.1% HL) (Tables 9, 12).

##### ***Coregonus acrinus*—*Coregonus wartmanni***

*Coregonus acrinus* differs from *C. wartmanni* by having a larger eye and eye cavity (eye diameter: 21.6–25.5% HL, mean = 23.7 vs. 18.9% HL; eye cavity: 26–29.6% HL, mean = 27.7 vs. 23.9% HL; eye height: 21.7–24.8% HL, mean = 22.9 vs. 19% HL) (Tables 9, 12).

##### ***Coregonus acrinus*—*Coregonus macrophthalmus***

*Coregonus acrinus* differs from *C. macrophthalmus* by having a wider head (43.9–56.2% HL, mean = 49.6 vs. 39.3–43.3% HL, mean = 41.6) (Tables 9, 12).

##### ***Coregonus acrinus*—*Coregonus gutturosus***

*Coregonus acrinus* differs from *C. gutturosus* by having more and longer gill rakers (upper arch gill raker number: 10–15, mode = 13 vs. 7–9, mode = 7; lower arch gill raker number: 20–26, mode = 24 vs. 9–12, mode = 10; total gill raker number: 30–40, mode = 36 vs. 16–21, mode = 19; middle gill raker length: 9.1–16.6% HL, mean = 13.4 vs. 4.1–8.7% HL, mean = 6.9; longest gill raker length: 11.4–16.9, mean = 14.5 vs. 6.7–10.6% HL, mean = 8.2), a longer lower jaw (38.6–47% HL, mean = 40.9 vs. 34.3–39.1% HL, mean = 36.6) and a shorter head (13.8–16.1% HL, mean = 15.2 vs. 15.4–18.1% HL, mean = 16.8) (Tables 9, 12, Suppl. material 1: Table S7).

##### ***Coregonus acrinus*—*Coregonus arenicolus***

*Coregonus acrinus* can be differentiated from *C. arenicolus* by having more and longer gill rakers (lower arch gill raker number: 20–26, mode = 24 vs. 13–19;

**Table 9.** Morphological and meristic data of *C. acrinus* from Lake Thun, NMBE-1077271, male, holotype; paratypes N = 25. For males and for both sexes, the range and mean include the holotype.

| Morphological characters             | <i>C. acrinus</i><br>Holotype | Lake Thun            |             |                       |             |                      |               |
|--------------------------------------|-------------------------------|----------------------|-------------|-----------------------|-------------|----------------------|---------------|
|                                      |                               | Both sexes           |             |                       |             |                      |               |
|                                      |                               | <i>N</i> -total = 26 |             | <i>N</i> -females = 4 |             | <i>N</i> -males = 22 |               |
|                                      | Mean±Stdev                    | Range                | Mean±Stdev  | Range                 | Mean±Stdev  | Range                |               |
| SL (mm)                              | 239.5                         | 237.3±21.2           | (197–278)   | 235.5±26.5            | (197–254)   | 237.6±20.8           | (197–278)     |
| <b>Percentage of standard length</b> |                               |                      |             |                       |             |                      |               |
| PelvFB                               | 5.1                           | 4.1±0.4              | (3.5–5.1)   | 3.7±0.4               | (3.5–4.3)   | 4.1±0.4              | (3.5–5.1)     |
| PelvFS                               | 7                             | 6.2±0.7              | (4.6–7.5)   | 6.2±0.3               | (5.7–6.4)   | 6.2±0.7              | (4.6–7.5)     |
| PelvF                                | 17.4                          | 16±0.9               | (14.3–17.5) | 15.6±1.2              | (14.6–17.2) | 16.1±0.8             | (14.3–17.5)   |
| PecFB                                | 3.6                           | 3.4±0.2              | (3.1–4.0)   | 3.2±0.1               | (3.1–3.4)   | 3.5±0.2              | (3.1–4)       |
| PecF1                                | 17.4                          | 15.9±1.1             | (13.8–18.2) | 15.6±1.8              | (14.1–18.1) | 16±1                 | (13.8–18.2)   |
| PecF2                                | 18.6                          | 16.9±1.3             | (15–19.7)   | 16.5±2.2              | (15–19.7)   | 17±1.1               | (15–19)       |
| DFB                                  | 14.8                          | 12.4±0.8             | (11.2–14.8) | 12.3±0.8              | (11.5–13.4) | 12.4±0.9             | (11.2–14.8)   |
| DFAc                                 | 20.9                          | 18.1±1.2             | (15.7–20.9) | 17.8±1.5              | (15.8–19.1) | 18.1±1.2             | (15.7–20.9)   |
| DFAd                                 | 21.7                          | 19.3±1.1             | (17.0–21.7) | 19.1±1.1              | (18.0–20.3) | 19.3±1.2             | (17–21.7)     |
| DFPe                                 | 5.5                           | 5.0±0.5              | (4.0–6.1)   | 4.9±0.5               | (4.2–5.3)   | 5±0.5                | (4–6.1)       |
| AFB                                  | 13.6                          | 12.6±0.6             | (11.3–13.6) | 12.6±0.6              | (11.9–13.3) | 12.6±0.6             | (11.3–13.6)   |
| AFAc                                 | 13                            | 11.6±0.8             | (9.2–13.0)  | 11.4±0.5              | (11.0–12.2) | 11.7±0.9             | (9.2–13)      |
| AdFB                                 | 4.5                           | 4.7±0.7              | (3.7–6.2)   | 4.8±0.6               | (4.2–5.6)   | 4.7±0.7              | (3.7–6.2)     |
| CF                                   | 24                            | 23.3±0.9             | (21.5–25.1) | 23.2±0.2              | (23–23.4)   | 23.4±1               | (21.5–25.1)   |
| CD                                   | 7.5                           | 7.6±0.4              | (7.1–8.3)   | 7.8±0.3               | (7.6–8.2)   | 7.6±0.4              | (7.1–8.3)     |
| CL                                   | 11.7                          | 12.8±0.6             | (11.7–14.2) | 12.4±0.4              | (11.9–12.8) | 12.9±0.6             | (11.7–14.2)   |
| PaDc                                 | 15                            | 18.1±1.2             | (15–20.1)   | 17.6±1                | (16.2–18.4) | 18.2±1.2             | (15–20.1)     |
| DHL                                  | 14.9                          | 15.2±0.6             | (13.8–16.1) | 14.9±0.9              | (14.0–15.9) | 15.2±0.5             | (13.8–16.1)   |
| PreP                                 | 50.3                          | 52.6±1.6             | (49.1–56.8) | 51.9±0.5              | (51.4–52.4) | 52.7±1.8             | (49.1–56.8)   |
| PreA                                 | 78.5                          | 77.7±1.2             | (75.3–80.3) | 77.1±0.5              | (76.5–77.6) | 77.8±1.3             | (75.3–80.3)   |
| PreD                                 | 45.4                          | 47.5±1.4             | (45–50.7)   | 47.5±1.1              | (46.3–48.6) | 47.5±1.4             | (45–50.7)     |
| BD                                   | 25.6                          | 24.7±1.6             | (20.7–28.1) | 26.1±1.6              | (24.4–28.1) | 24.4±1.5             | (20.7–26.7)   |
| PostD                                | 41.2                          | 43±1.3               | (40.3–45.6) | 42.2±1.6              | (41–44.3)   | 43.1±1.3             | (40.3–45.6)   |
| TL                                   | 123.2                         | 120.6±1.7            | (116–123.2) | 119±2.5               | (116–121.5) | 120.8±1.4            | (118.2–123.2) |
| HL (mm)                              | 49                            | 49.9±4               | (41.5–58.4) | 48.5±4.7              | (41.5–51.3) | 50.1±3.9             | (41.5–58.4)   |
| <b>Percentage of head length</b>     |                               |                      |             |                       |             |                      |               |
| SN                                   | 23.4                          | 23.9±1.4             | (20.5–27)   | 22.6±1.8              | (20.5–24.6) | 24.1±1.3             | (21.6–27)     |
| ED                                   | 23.2                          | 23.7±0.8             | (21.6–25.5) | 23.8±0.8              | (22.6–24.4) | 23.7±0.9             | (21.6–25.5)   |
| EC                                   | 27.4                          | 27.7±1               | (26–29.6)   | 28.6±1                | (27.2–29.6) | 27.6±0.9             | (26–28.8)     |
| EH                                   | 22.8                          | 22.9±0.9             | (21.7–24.8) | 23.6±1.1              | (22.2–24.8) | 22.8±0.8             | (21.7–24.5)   |
| ES                                   | 4.9                           | 4.7±0.8              | (3.2–6.4)   | 5.6±0.9               | (4.8–6.4)   | 4.5±0.6              | (3.2–6.1)     |
| PostO                                | 51                            | 50.9±1.5             | (48.5–54.1) | 52±1.8                | (49.8–54.1) | 50.7±1.4             | (48.5–53)     |
| HD                                   | 69.8                          | 69.1±2.4             | (65.1–74.9) | 69.8±2                | (67.8–72.5) | 68.9±2.5             | (65.1–74.9)   |
| MW                                   | 9.7                           | 9.8±0.7              | (8.1–11.4)  | 9.8±0.6               | (8.8–10.3)  | 9.8±0.8              | (8.1–11.4)    |
| UJ                                   | 28.8                          | 29.4±1.2             | (26.7–30.9) | 30.1±0.8              | (29.3–30.8) | 29.2±1.3             | (26.7–30.9)   |
| LJ                                   | 40.5                          | 40.9±1.7             | (38.6–47)   | 40.5±1.1              | (39–41.5)   | 41±1.8               | (38.6–47)     |
| M                                    | 21.1                          | 21.8±1               | (19.4–23.8) | 21.9±0.9              | (21.3–23.2) | 21.8±1               | (19.4–23.8)   |
| SD                                   | 9.8                           | 8.6±1.3              | (6–11.3)    | 9±1.1                 | (7.9–10.5)  | 8.6±1.3              | (6–11.3)      |
| SW                                   | 17.1                          | 16±1.5               | (13.1–18.1) | 16.2±1.3              | (14.7–17.6) | 15.9±1.5             | (13.1–18.1)   |
| HW                                   | 53.8                          | 49.6±3.2             | (43.9–56.2) | 51.1±2.4              | (48.2–53.8) | 49.4±3.3             | (43.9–56.2)   |
| IOW                                  | 25.8                          | 27±2.1               | (21.3–31.5) | 27.1±1.4              | (25.1–28.1) | 27±2.3               | (21.3–31.5)   |
| INW                                  | 10.8                          | 11.7±1               | (9.5–13.4)  | 11.7±1.2              | (10.5–13.3) | 11.7±1               | (9.5–13.4)    |
| LJW                                  | 12.4                          | 12.2±1.2             | (9.2–14.3)  | 12.5±1                | (11–13.4)   | 12.1±1.2             | (9.2–14.3)    |
| UJW                                  | 24                            | 22.8±2.1             | (18.2–27.5) | 23.7±2.7              | (20.4–26.3) | 22.6±2               | (18.2–27.5)   |
| MGR                                  | 13.1                          | 13.4±1.6             | (9.1–16.6)  | 14.4±1.9              | (11.9–16.6) | 13.2±1.6             | (9.1–15.1)    |
| LGR                                  | 15                            | 14.5±1.4             | (11.4–16.9) | 15.7±1.2              | (14.4–16.9) | 14.3±1.3             | (11.4–16.3)   |
| UA                                   | 19.7                          | 18.1±1.6             | (13.5–20.3) | 18.5±1.6              | (16.2–19.8) | 18.1±1.6             | (13.5–20.3)   |
| LA                                   | 36.7                          | 34.9±1.7             | (32.3–38.9) | 35.9±2.1              | (34–38.9)   | 34.8±1.7             | (32.3–38.4)   |
| <b>Meristic characters</b>           |                               |                      |             |                       |             |                      |               |
|                                      |                               | Mode                 | Range       | Mode                  | Range       | Mode                 | Range         |
| PelvF unbranched                     | 1                             | 1                    | (1–1)       | 1                     | (1–1)       | 1                    | (1–1)         |
| PelvF branched                       | 11                            | 10                   | (9–12)      | 10                    | (10–11)     | 11                   | (9–12)        |
| PecF unbranched                      | 1                             | 1                    | (1–1)       | 1                     | (1–1)       | 1                    | (1–1)         |
| PecF branched                        | 15                            | 15                   | (13–16)     | 16                    | (15–16)     | 15                   | (13–16)       |

| Meristic characters | <i>C. acrinus</i><br>Holotype | Lake Thun            |         |                       |         |                      |         |
|---------------------|-------------------------------|----------------------|---------|-----------------------|---------|----------------------|---------|
|                     |                               | Both sexes           |         |                       |         |                      |         |
|                     |                               | <i>N</i> -total = 26 |         | <i>N</i> -females = 4 |         | <i>N</i> -males = 22 |         |
|                     |                               | Mode                 | Range   | Mode                  | Range   | Mode                 | Range   |
| DF unbranched       | 3                             | 4                    | (3–4)   | 3                     | (3–4)   | 4                    | (3–4)   |
| DF branched         | 12                            | 10                   | (9–12)  | 11                    | (10–12) | 10                   | (9–12)  |
| AF unbranched       | 3                             | 3                    | (2–4)   | 3                     | (3–3)   | 3                    | (2–4)   |
| AF branched         | 13                            | 11                   | (11–13) | 12                    | (11–13) | 11                   | (11–13) |
| LS                  | 80                            | 84                   | (79–88) | 85                    | (84–85) | 80                   | (79–88) |
| PDS                 | 34                            | 34                   | (33–42) | 34                    | (34–41) | 35                   | (33–42) |
| TDS                 | 10                            | 10                   | (9–10)  | 10                    | (9–10)  | 10                   | (9–10)  |
| TAS                 | 8                             | 8                    | (8–9)   | 8                     | (8–8)   | 8                    | (8–9)   |
| TPS                 | 9                             | 8                    | (8–9)   | 9                     | (8–9)   | 8                    | (8–9)   |
| UGR                 | 13                            | 13                   | (10–15) | na                    | (10–15) | 13                   | (10–14) |
| LGR                 | 20                            | 24                   | (20–26) | 24                    | (21–24) | 24                   | (20–26) |
| total GR            | 33                            | 36                   | (30–40) | 35                    | (34–36) | 36                   | (30–40) |

total gill raker number: 30–40, mode = 36 vs. 22–31; middle gill raker length: 9.1–16.6% HL, mean = 13.4 vs. 9.8–10.6% HL, mean = 10.2; longest gill raker length: 11.4–16.9, mean = 14.5 vs. 10.9–12% HL, mean = 11.5), a larger eye (eye diameter: 21.6–25.5% HL, mean = 23.7 vs. 17.3–19.6% HL, mean = 17.7; eye cavity: 26–29.6% HL, mean = 27.7 vs. 24.1–25.7% HL, mean = 25; eye height: 21.7–24.8% HL, mean = 22.9 vs. 18.8–20.8% HL, mean = 19.6) and a shorter anal fin (9.2–13% HL, mean = 11.6 vs. 12.9–13.8% HL, mean = 13.3) (Tables 9, 12, Suppl. material 1: Table S7).

**Description.** General appearance is shown in Figure 10. Morphological and meristic characters of both sexes can be found in Tables 9, 12, and Suppl. material 1: Tables S6, S7 and first- and second-best ratios for both sexes combined can be found in Table 10. The description is valid for both sexes.

**Shape:** Only slightly deep bodied with greatest body depth anterior of the dorsal fin. Dorsal and ventral profile equally arched such that both the dorsal profile from the tip of snout to the anterior origin of dorsal fin and the ventral profile from the interorbital area to the pelvic fin origin are moderately convex. Head long. Mouth (i.e., width of upper and lower jaw) is thick, moderately long and often sub-terminal and only rarely terminal. Rostral plate is mostly wider than deep, not strongly pronounced and the tip of the snout is often pointy in the sagittal plane. Eye-socket thick and triangular (i.e., sickle-shaped). Pectoral fin moderately tapered. Anterior unbranched ray of the erected dorsal fin has an approx. 40–60° angle to body axis and from the middle to the end of the ray it is moderately bent posteriorly. Caudal peduncle stout and moderately long. Caudal fin forked and sometimes slightly asymmetrical with the ventral part being longer. Unbranched ray of anal fin mostly straight and only sometimes slightly bent posteriorly. Anal fin is longest anteriorly and progressively shortening posteriorly with the outer margin of the anal fin slightly concave.

**Meristics:** Many and moderately long gill rakers.

**Colour:** Pigmentation of fins and body overall moderately strong in live specimens. Pectoral fin is mostly transparent to moderately pigmented with a yellowish faint pigmentation and only very rarely strongly pigmented. Dorsal, adipose, pelvic, anal, and caudal fins are moderately to strongly pigmented. Fish have a silvery ap-

pearance along the flanks with moderate to many pigmented small dots on the scales. Dots along the flank and the dorsum. Distribution of the dots is bound to the scale patterning such that the dots are found at the edge of the scales or at the boundary point of two scales. Dorsally above the lateral line the silvery appearance changes to dark greenish blue colour (e.g., RGB (7,168,125)). The snout around the nostrils is strongly pigmented with a gap of very little pigmentation posteriorly of the nostrils up to the height of the middle of the eyes. Pre-operculum and operculum are silvery with one black dot on the lower margin of the pre-operculum. For a comparison to the main colouration found in the other species see Suppl. material 1: Figure S8. Preserved specimens are pale in colouration with similar pigmentation as described for live specimens. Silvery, translucent, not coloured or unpigmented parts of the body become brown-yellowish (e.g., RGB (239, 210, 40)), whereas the pigmented parts are conserved and the coloured parts (dorsally above the lateral line) become brownish (e.g., RGB (186, 140, 100)).

**Distribution and notes on biology.** *Coregonus acrinus* is found in Lake Thun (46°40'N, 7°46'E). Based on isotopic signatures *C. acrinus* most likely feeds on a mix of benthic prey and zooplankton (Selz 2008; Hudson 2011; Ingram et al. 2012) and based on the size-at-age data *C. acrinus* must have a rather fast growth rate (Suppl. material 1: Figures S4–S6). The gill raker number and length of *C. acrinus* (many gill rakers and moderately long gill rakers) suggests, based on the functional properties of the number of gill rakers on feeding on different prey items (Lundsgaard-Hansen et al. 2013; Roesch et al. 2013), that *C. acrinus* feeds more on zooplankton and less on benthic prey, but this assumption needs to be verified in the future with stomach content analyses. The relative species abundances in the pelagic and benthic habitat from a habitat-stratified random sampling of Lake Thun (mid-October 2013: Vonlanthen et al. 2015) also points to this. *Coregonus acrinus* occupies only the shallow waters of the benthic habitat (15 m;  $N = 1$ ) and the moderately deep pelagic waters (approx. 10–35 m;  $N = 9$ ) (Dönz et al. 2018). However, the habitat-stratified sampling needs to be treated with caution since it only shows a snapshot in time (one month) of the spatial distribution of this and the other species. *Coregonus acrinus* phenotypically resembles to some extent *C. alpinus* and *C. steinmanni*. The average size (total length) at three years of age for specimens in this study of *C. acrinus* is  $304 \pm 21$  mm (mean and standard deviation,  $N = 9$ ) (Suppl. material 1: Figures S4, S6). The average size at 3 years of age for the specimens of *C. acrinus* from this study is similar to that for the years 2004–2005 ( $322.8 \pm 18$  mm,  $N = 50$ ) (Bittner et al. unpublished; Vonlanthen et al. unpublished). The size of 3-year-old specimens of *C. acrinus* is smaller to that of *C. alpinus* and *C. steinmanni* and considerably larger than that of *C. albellus*, *C. fatioides*, and *C. profundus* (Suppl. material 1: Figure S6). *Coregonus acrinus* has a short spawning season in late December and very rarely have ripe individuals been caught in late autumn or winter (Suppl. material 1: Figure S3; Dönz et al. 2018). *Coregonus acrinus* spawns mostly in moderately shallow waters of 10m down to approx. 100 m (Suppl. material 1: Figure S3; Bittner 2009; Dönz et al. 2018). The spawning season and depth of *C. acrinus* overlaps

largely with that of *C. alpinus*, *C. steinmanni*, and *C. fatioi* and to a much lesser extent with that of *C. albellus* and *C. profundus*.

*Coregonus acrinus* appears to be a species of partially allochthonous origin, closely related to the radiation of Lake Constance with genetic contributions from Lake Thun. Indications of this situation were seen in several earlier genetic studies (Douglas and Brunner 2002; Douglas et al. 2003; Bittner 2009; Hudson et al. 2011) and this was clearly confirmed with large sample sizes recently (Hudson et al. 2016; Dönz et al. 2018). Historical records mention the stocking of alevins of the Lake Constance endemics *C. wartmanni* and *C. macrophthalmus* into Lake Thun. To fully understand the relationship of *C. acrinus* to the Lake Constance species, we compared the morphology of *C. acrinus* with that of all four described species of Lake Constance, *C. wartmanni*, *C. macrophthalmus*, *C. arenicolus*, and the now extinct *C. gutturosus*. Our data clearly reveal *C. acrinus* as distinct from all Lake Constance species based on morphological characters. Historical records from Fatio (1890) in his book on Swiss fish (Fatio 1890: Page 123) and from Heuscher (1901) in his report on the biology of lakes Thun and Brienz (Heuscher 1901: Pages 69–70, 103) report several incidences of introductions of whitefish from other lakes. Evidence for additional introductions comes from historical records from a fisheries club that was responsible for the propagation of whitefish in lakes Thun and Brienz before stocking with allochthonous fish was forbidden in Lake Thun (nothing is stated regarding Lake Brienz) in 1946 by the local fisheries authorities (Douglas et al. 2003; Dönz et al. 2018). Since 1991 such introductions were banned in all of Switzerland through federal law (BGF 6 I b). These historical records reveal that in 1888, 1889, and 1934 in Lake Thun and 1892 in Lake Brienz between 20'000 and 750'000 (Lake Thun) and once 39'000 (Lake Brienz) fry of either *C. macrophthalmus* (only Lake Thun) or *C. wartmanni* (both lakes) were stocked. Heuscher (1901: Page 70) further noted that the introductions of 1888, 1889, and 1892 were unsuccessful in both lakes, as fishermen did not catch adult fish of either of the Lake Constance species ever after those introductions. Steinmann (1950) in his monograph on Swiss whitefish diversity did not mention any species from Lake Constance to be present in Lake Thun or in Lake Brienz. Dönz et al. (2018) could recently show with genetic data from scales dating back to 1972 and earlier that *C. acrinus* was completely absent in catches of that period. The first qualitative reports of this species in spawning fisheries catches are from around the year 2000 (Douglas et al. 1999; Bittner 2009), and our own genetic data from samples of more than 2000 whitefish from Lake Thun confirm the presence of the species. Based on a recent lake-wide quantitative survey in 2015 Dönz et al. (2018) showed that this species accounts for ca. 10% of all whitefish in Lake Thun in abundance when based on genetic assignments. Several independent multilocus microsatellite and AFLP data sets suggest that it has genetic contributions from the endemic Lake Thun species and cannot clearly be designated genetically to one of the Lake Constance species (Douglas and Brunner 2002; Douglas et al. 2003; Bittner 2009; Hudson et al. 2011; Hudson et al. 2016; Dönz et al. 2018). This suggests that some individuals of one or several of the introduced species from Lake



**Figure 10.** *Coregonus acrinastus*, Lake Thun, Switzerland **A** holotype, NMBE-1077271, Lake Thun, 239.5 mm SL, male, freshly caught specimen **B, C** holotype, NMBE-1077271, preserved specimen **D** paratype, NMBE-1077270, Lake Thun, 270 mm SL, male, freshly caught specimen **E** paratype, NMBE-1077279, Lake Thun, 234 mm SL, male, freshly caught specimen. The white scale (1cm) below each fish acts as a reference for the actual size of the specimen.

Constance must have successfully reproduced in Lake Thun and hybridized with one or several of the local species.

**Etymology.** The name *C. acrinasus* is a combination of the ablative case of the Latin adjective *acer* resulting in *acri*, which means pointed and the noun *nasus* for nose. The name acrinasus refers to a phenotypic feature of this species, which often has a pointed snout when viewed in the sagittal plane.

**Common name.** Albock

### Lake Constance whitefish species

#### *Coregonus gutturosus*, Gmelin, 1818

##### Figure 11

**Material examined. Non-types.** NMBE-1076230 (Eawag-246), NMBE-1076232 (Eawag-248-1), NMBE-1076233 (N = 6: Eawag-249-1, Eawag-249-2, Eawag-249-3, Eawag-249-4, Eawag-249-5, Eawag-249-6), NMBE-1076232 (N = 2: Eawag-248-2, Eawag-248-3), Switzerland, Lake Constance (47°38'N, 9°22'E), N = 10, 169–292 mm SL.

**Distribution and notes on biology.** *Coregonus gutturosus* used to be endemic to Lake Constance but is now extinct.

**Common name.** Kilch

#### *Coregonus arenicolus*, Kottelat, 1997

##### Figure 11

**Material examined. Holotype.** NMBE-1076223 (Eawag-239-1), Switzerland, Lake Constance (47°38'N, 9°22'E), 296 mm SL, sex unknown.

**Paratypes.** NMBE-1076223 (N = 3: Eawag-239-2, Eawag-239-3, Eawag-239-4), Switzerland, Lake Constance (47°38'N, 9°22'E), N = 3, 289–314 mm SL.

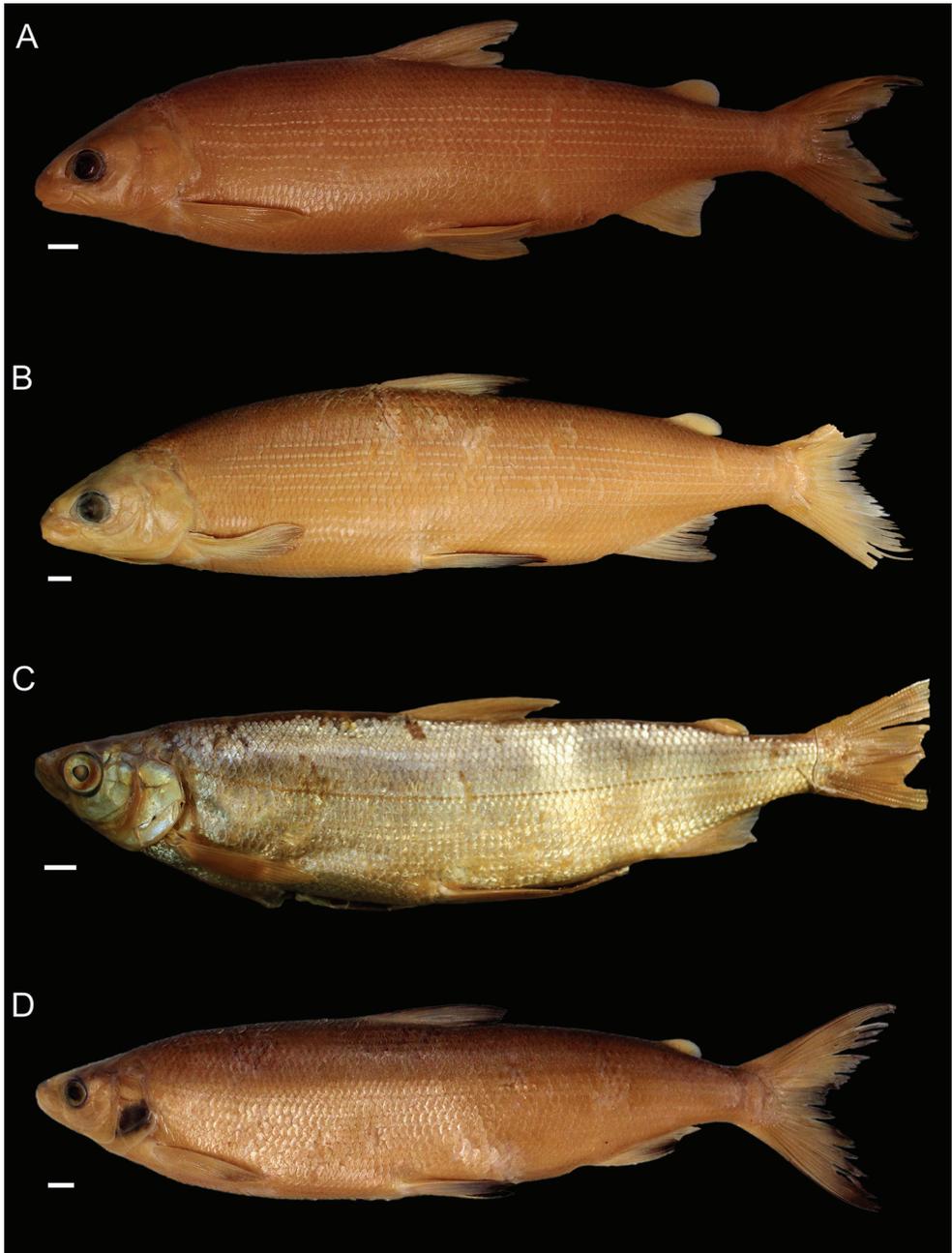
**Distribution and notes on biology.** *Coregonus arenicolus* is found in the upper and lower basin of Lake Constance.

**Common name.** Sandfelchen.

#### *Coregonus macrophthalmus*, Nüsslin, 1882

##### Figure 11

**Material examined. Syntypes.** MHNG-716.052, MHNG-716.051, MHNG-816.02, MHNG-715.094 (N = 2: MHNG-715.094-1, MHNG-715.094-2), NMBE-1076211 (N = 2: Eawag-227-1, Eawag-227-2), Switzerland, Lake Constance (47°38'N, 9°22'E), N = 7, 193–235 mm SL.



**Figure 11.** Types of the Lake Constance species, Switzerland **A** *Coregonus gutturosus*, non-type, NMBE-1076232 (Eawag-248–1), 250 mm, sex unknown, preserved specimen **B** *Coregonus arenicolus*, holotype, 296 mm, NMBE-1076223 (Eawag-239–1), sex unknown, preserved specimen **C** *Coregonus macrophthalmus*, syntype, MHNG-716.052, 215 mm, sex unknown, preserved specimen **D** *Coregonus wartmanni*, non-type, NMBE-1076206, 301 mm, female, preserved specimen. The white scale (1cm) below each fish acts as a reference for the actual size of the specimen.

**Table 10.** The first- and second-best ratios retrieved from the LDA ratio extractor of either head or body characters (see Table 1) alone or combined, used for pair-wise comparisons of all contemporary specimens from the six whitefish species of Lake Thun. For some comparisons only a subset of characters could be used (a-d); the respective characters that were excluded are listed at the end of the table. Only external characters were used for the LDA comparisons, since internal characters (gill raker and gill arch length) cannot be measured on live specimens, and are thus not informative to assign specimens to species in the field. Additionally, species were combined to find first- and second-best ratios that distinguish one species or a combination of species vs. all other species. For multi-species comparisons, only the comparisons that yielded distinguishing ratios are shown.  $\delta$  is a measure of how good shape discriminates in comparison to size (i.e., the smaller  $\delta$  the less allometry). Ratios marked with an asterisk \* have very little (for the pairwise species comparisons not more than one specimen of one species overlaps with the other species) or no overlap and were thus eligible for use in the species key and the diagnoses.

| Characters  | Species comparison                             | Best ratios    | Range species 1 | Range species 2 | Standard distance | $\delta$ (Shape vs. size) |
|-------------|--|----------------|-----------------|-----------------|-------------------|---------------------------|
| head + body | <i>C. albellus</i> vs. <i>C. alpinus</i>       | 1: CD/UJ *     | 0.96–1.29       | 1.36–1.65       | 18.09             | 0.1                       |
|             |  | 2: AdFB/ES     | 5.54–13.54      | 2.87–5.94       | 17.49             | 0.1                       |
| body        | <i>C. albellus</i> vs. <i>C. alpinus</i>       | 1: CD/DHL *    | 0.44–0.54       | 0.54–0.62       | 5.98              | 0.26                      |
|             |  | 2: DFB/AdFB    | 1.6–2.66        | 2.31–4.02       | 4.86              | 0.31                      |
| head        | <i>C. albellus</i> vs. <i>C. alpinus</i>       | 1: UJ/ES       | 6.48–16.01      | 4.52–7.93       | 6                 | 0.22                      |
|             |  | 2: HL/UJ       | 2.88–3.47       | 3.33–4.11       | 5.26              | 0.25                      |
| head + body | <i>C. albellus</i> vs. <i>C. fatioi</i>        | 1: TL/EH       | 21.93–27.57     | 21.91–29.46     | 3.07              | 0.08                      |
|             |  | 2: PelvF/PecF1 | 0.87–1.03       | 0.87–1.07       | 2.89              | 0.08                      |
| body        | <i>C. albellus</i> vs. <i>C. fatioi</i>        | 1: PecF1/TL    | 0.12–0.16       | 0.11–0.15       | 1.4               | 0.19                      |
|             |  | 2: DFAe/DFAAd  | 0.88–1          | 0.9–0.98        | 1.18              | 0.21                      |
| head        | <i>C. albellus</i> vs. <i>C. fatioi</i>        | 1: EH/HL       | 0.21–0.26       | 0.2–0.25        | 1.63              | 0.08                      |
|             |  | 2: LJW/ES      | 2.14–7.79       | 1.59–8.18       | 1.35              | 0.1                       |
| head + body | <i>C. albellus</i> vs. <i>C. steinmanni</i>    | 1: CD/UJ *     | 0.96–1.29       | 1.36–1.55       | 13.8              | 0.12                      |
|             |  | 2: AdFB/ES     | 5.54–13.54      | 3.31–6.31       | 13                | 0.12                      |
| head        | <i>C. albellus</i> vs. <i>C. steinmanni</i>    | 1: HL/UJ       | 2.88–3.47       | 3.33–3.97       | 5.3               | 0.21                      |
|             |  | 2: LJ/ES       | 8.25–20.33      | 6.65–12.45      | 4.59              | 0.23                      |
| head + body | <i>C. albellus</i> vs. <i>C. profundus</i>     | 1: CL/EC *     | 1.97–2.87       | 1.56–2.09       | 13.19             | 0.03                      |
|             |  | 2: DHL/M       | 2.77–3.53       | 3.21–3.79       | 12.79             | 0.03                      |
| body        | <i>C. albellus</i> vs. <i>C. profundus</i>     | 1: CL/DHL      | 0.75–1.04       | 0.61–0.82       | 4.43              | 0.06                      |
|             |  | 2: CD/BD       | 0.26–0.31       | 0.28–0.34       | 3.38              | 0.07                      |
| head        | <i>C. albellus</i> vs. <i>C. profundus</i>     | 1: EC/UJ       | 0.74–0.95       | 0.87–1.05       | 5.02              | 0.1                       |
|             |  | 2: SW/ES       | 3.22–9.67       | 2.31–5.26       | 4.05              | 0.12                      |
| head + body | <i>C. albellus</i> vs. <i>C. acrinus</i>       | 1: AdFB/ES     | 5.54–13.54      | 3.31–6.5        | 9.13              | 0.06                      |
|             |  | 2: CD/UJW      | 1.14–1.79       | 1.4–2           | 8.69              | 0.07                      |
| body        | <i>C. albellus</i> vs. <i>C. acrinus</i>       | 1: PecF1/CD    | 2.13–2.76       | 1.8–2.39        | 4.5               | 0.11                      |
|             |  | 2: DFB/AdFB    | 1.6–2.66        | 1.98–3.45       | 3.88              | 0.13                      |
| head        | <i>C. albellus</i> vs. <i>C. acrinus</i>       | 1: UJW/ES      | 5.27–13.65      | 3.22–7.96       | 4.19              | 0.14                      |
|             |  | 2: ED/UJ       | 0.66–0.84       | 0.74–0.9        | 3.51              | 0.16                      |
| Characters  | Species comparison                             | Best ratios    | Range species 1 | Range species 2 | Standard distance | $\delta$ (shape vs. Size) |
| head + body | <i>C. alpinus</i> vs. <i>C. fatioi</i>         | 1: CD/PostD *  | 0.17–0.21       | 0.14–0.17       | 22.73             | 0.07                      |
|             |  | 2: DFAe/UJ     | 3.14–3.93       | 2.43–3.41       | 22.33             | 0.07                      |
| body        | <i>C. alpinus</i> vs. <i>C. fatioi</i>         | 1: CD/PostD *  | 0.17–0.21       | 0.14–0.17       | 8.98              | 0.17                      |
|             |  | 2: DFAe/DHL    | 1.26–1.55       | 1.02–1.36       | 7.9               | 0.19                      |
| head        | <i>C. alpinus</i> vs. <i>C. fatioi</i>         | 1: HD/UJ       | 2.34–2.9        | 2.13–2.57       | 3.86              | 0.3                       |
|             |  | 2: MW/ES       | 1.47–3          | 1.82–6.16       | 3.15              | 0.34                      |
| head + body | <i>C. alpinus</i> vs. <i>C. steinmanni</i> (a) | ED/EC          | 0.74–0.9        | 0.74–0.9        | 8.07              | 0.05                      |
|             |  | CD/CL          | 0.6–0.75        | 0.54–0.7        | 8.02              | 0.05                      |
| body        | <i>C. alpinus</i> vs. <i>C. steinmanni</i>     | 1: DFAe/AFAe   | 1.5–1.83        | 1.43–1.62       | 5.7               | 0.06                      |
|             |  | 2: PelvFS/DFAe | 0.24–0.36       | 0.29–0.37       | 5.58              | 0.07                      |
| head        | <i>C. alpinus</i> vs. <i>C. steinmanni</i>     | 1: EC/SW       | 1.47–2.13       | 1.43–1.7        | 2.45              | 0.16                      |
|             |  | 2: ED/EC       | 0.74–0.9        | 0.79–0.9        | 2.2               | 0.18                      |
| head + body | <i>C. alpinus</i> vs. <i>C. profundus</i>      | 1: CD/DHL *    | 0.54–0.62       | 0.4–0.49        | 19.86             | 0.07                      |
|             |  | 2: PecF2/CF    | 0.63–0.82       | 0.74–0.90       | 19.01             | 0.07                      |

| Characters  | Species comparison   | Best ratios   | Range species 1 | Range species 2 | Standard distance | δ (Shape vs. size) |
|-------------|--|---------------|-----------------|-----------------|-------------------|--------------------|
| body        | <i>C. alpinus</i> vs. <i>C. profundus</i>                    | 1: CD/DHL *   | 0.54–0.62       | 0.4–0.49        | 9.31              | 0.15               |
|             |  | 2: PecF2/CF   | 0.63–0.82       | 0.74–0.90       | 7.32              | 0.19               |
| head        | <i>C. alpinus</i> vs. <i>C. profundus</i>                    | 1: EH/PostD   | 0.09–0.11       | 0.11–0.15       | 4.32              | 0.21               |
|             |  | 2: SD/UJW     | 0.35–0.51       | 0.30–0.44       | 3.93              | 0.23               |
| head + body | <i>C. alpinus</i> vs. <i>C. acrinasus</i>                    | 1: CD/LJ      | 0.95–1.11       | 0.79–1          | 65.21             | 0.02               |
|             |  | 2: CF/M *     | 5.55–6.55       | 4.4–5.57        | 65.13             | 0.02               |
| body        | <i>C. alpinus</i> vs. <i>C. acrinasus</i>                    | 1: CD/DHL     | 0.54–0.62       | 0.46–0.58       | 4.69              | 0.25               |
|             |  | 2: DFAe/DFPe  | 3.39–4.72       | 2.84–4.54       | 3.91              | 0.29               |
| head        | <i>C. alpinus</i> vs. <i>C. acrinasus</i>                    | 1: PostO/M    | 2.4–3           | 2.17–2.56       | 4.26              | 0.21               |
|             |  | 2: HD/MW      | 6.57–8.7        | 6.02–8.87       | 3.65              | 0.24               |
| Characters  | Species comparison   | Best ratios   | Range species 1 | Range species 2 | Standard distance | δ (shape vs. Size) |
| head + body | <i>C. fatioi</i> vs. <i>C. steinmanni</i> (b)                | 1: CD/UJ *    | 1.02–1.34       | 1.36–1.55       | 33.96             | 0.04               |
|             |  | 2: PelvF/PAdC | 0.73–1          | 0.84–0.1        | 33.71             | 0.04               |
| body        | <i>C. fatioi</i> vs. <i>C. steinmanni</i>                    | 1: CD/PostD * | 0.14–0.17       | 0.17–0.20       | 6.34              | 0.22               |
|             |  | 2: DHL/BD     | 0.5–0.7         | 0.45–0.58       | 5.37              | 0.25               |
| head        | <i>C. fatioi</i> vs. <i>C. steinmanni</i>                    | 1: HD/UJ      | 2.13–2.57       | 2.42–2.83       | 4.41              | 0.23               |
|             |  | 2: HW/LJW     | 3.17–6.12       | 3.72–5.1        | 3.25              | 0.29               |
| head + body | <i>C. fatioi</i> vs. <i>C. profundus</i>                     | 1: CL/EC      | 1.84–2.98       | 1.56–2.09       | 10.03             | 0.02               |
|             |  | 2: DHL/UJ     | 2.11–2.70       | 2.32–2.92       | 9.54              | 0.02               |
| body        | <i>C. fatioi</i> vs. <i>C. profundus</i>                     | 1: CL/DHL     | 0.76–1.04       | 0.61–0.82       | 4.44              | <0.01              |
|             |  | 2: DFPe/CD    | 0.56–0.87       | 0.56–0.82       | 3.2               | <0.01              |
| head        | <i>C. fatioi</i> vs. <i>C. profundus</i>                     | 1: EC/SW      | 1.32–1.73       | 1.63–2.38       | 5.05              | 0.08               |
|             |  | 2: UJ/UJW     | 1.04–1.50       | 1–1.29          | 4.28              | 0.09               |
| head + body | <i>C. fatioi</i> vs. <i>C. acrinasus</i>                     | 1: CD/PostD   | 0.14–0.17       | 0.16–0.2        | 8.3               | 0.05               |
|             |  | 2: ED/SW      | 1.08–1.5        | 1.3–1.79        | 8                 | 0.05               |
| body        | <i>C. fatioi</i> vs. <i>C. acrinasus</i>                     | 1: CD/PostD   | 0.14–0.17       | 0.16–0.2        | 3.66              | 0.07               |
|             |  | 2: AFAe/DHL   | 0.69–0.9        | 0.61–0.93       | 2.93              | 0.09               |
| head        | <i>C. fatioi</i> vs. <i>C. acrinasus</i>                     | 1: ED/SW      | 1.08–1.5        | 1.3–1.79        | 3.05              | 0.15               |
|             |  | 2: MW/ES      | 1.82–6.16       | 1.4–3.02        | 2.45              | 0.18               |
| Characters  | Species comparison   | Best ratios   | Range species 1 | Range species 2 | Standard distance | δ (shape vs. Size) |
| head + body | <i>C. steinmanni</i> vs. <i>C. profundus</i> (c)             | 1: CD/DHL *   | 0.53–0.63       | 0.4–0.49        | 23.9              | 0.05               |
|             |  | 2: CL/IOW     | 2.05–2.69       | 1.69–2.28       | 23.3              | 0.05               |
| body        | <i>C. steinmanni</i> vs. <i>C. profundus</i>                 | 1: CD/DHL *   | 0.53–0.63       | 0.4–0.49        | 9.13              | 0.14               |
|             |  | 2: PecF2/DFAe | 0.76–0.96       | 0.82–1.21       | 7.44              | 0.17               |
| head        | <i>C. steinmanni</i> vs. <i>C. profundus</i>                 | 1: SW/UJW     | 0.65–0.80       | 0.54–0.69       | 5.9               | 0.12               |
|             |  | 2: EH/PostO   | 0.36–0.47       | 0.41–0.52       | 5.37              | 0.13               |
| head + body | <i>C. steinmanni</i> vs. <i>C. acrinasus</i> (d)             | 1: CD/M *     | 1.86–2.24       | 1.4–1.9         | 160.64            | <0.01              |
|             |  | 2: PostD/LJ   | 4.96–5.9        | 4.65–5.43       | 160.6             | <0.01              |
| body        | <i>C. steinmanni</i> vs. <i>C. acrinasus</i>                 | 1: CD/DHL     | 0.53–0.63       | 0.46–0.58       | 4.46              | 0.23               |
|             |  | 2: PelvF/DHL  | 1.08–1.26       | 0.95–1.16       | 3.83              | 0.26               |
| head        | <i>C. steinmanni</i> vs. <i>C. acrinasus</i>                 | 1: ED/HD      | 0.29–0.33       | 0.31–0.37       | 4.54              | 0.13               |
|             |  | 2: HL/M       | 4.6–5.53        | 4.21–5.17       | 3.41              | 0.17               |
| Characters  | Species comparison   | Best ratios   | Range species 1 | Range species 2 | Standard distance | δ (shape vs. Size) |
| head + body | <i>C. profundus</i> vs. <i>C. acrinasus</i>                  | 1: PecF2/CD   | 2.37–3.16       | 1.91–2.59       | 13.46             | 0.01               |
|             |  | 2: LJ/UJW     | 1.34–1.86       | 1.54–2.27       | 13.12             | 0.01               |
| body        | <i>C. profundus</i> vs. <i>C. acrinasus</i>                  | 1: PecF2/CD   | 2.37–3.16       | 1.91–2.59       | 4.58              | 0.05               |
|             |  | 2: DHL/TL     | 0.13–0.15       | 0.12–0.13       | 3.48              | 0.06               |
| head        | <i>C. profundus</i> vs. <i>C. acrinasus</i>                  | 1: M/UJW      | 0.69–0.94       | 0.8–1.22        | 4.45              | 0.02               |
|             |  | 2: EC/LJ      | 0.66–0.81       | 0.58–0.72       | 3.88              | 0.02               |
| Characters  | Multiple species comparison                                  | Best ratios   | Range group 1   | Range group 2   | Standard distance | δ (shape vs. Size) |
| head + body | <i>C. alpinus</i> + <i>C. steinmanni</i> vs. 4 other species | 1: CD/UJ *    | 1.36–1.65       | 0.96–1.43       | 5.34              | 0.24               |

(a) PelvFS, PecF1, DFAe, DFPe, TL, SL, EH, SD, SW, INW, IOW

(b) PelvFS, PecF1, DFAe, TL

(c) PelvFS, PecF1, DFAe, TL, EH

(d) PelvFS, PecF1, DFAe, TL, EH, ES, EC

**Table II.** The first- and second-best ratios retrieved from the LDA ratio extractor of either head or body characters (see Table 1) alone or combined, used for pair-wise comparisons of all contemporary specimens from the four whitefish species of Lake Brienz. For some species comparisons only a subset of characters could be used (a-l); the respective characters that were excluded are listed at the end of the table. Only external characters were used for the LDA comparisons, since internal characters (gill raker and gill arch length) cannot be measured on live specimens, and are thus not informative to assign specimens to species in the field. Due to large size differences between the species the LDA ratios were calculated with three different datasets; once each with individuals larger or smaller than 163.5mm standard length and once with the full size ranges of all species. For the multi-species comparisons, only the comparisons that yielded distinguishing ratios are shown.  $\delta$  is a measure of how good shape discriminates in comparison to size (i.e., the smaller the less allometry). Ratios marked with an asterisk \* have very little (for the pairwise species comparisons not more than one specimen of one species overlaps with that of the other species) or no overlap and were thus eligible for use in the species key and the diagnoses.

| Characters  | Species comparison                            | Size range | Best ratios     | Range species 1 | Range species 2 | Standard distance | $\delta$ (Shape vs. size) |
|-------------|---|------------|-----------------|-----------------|-----------------|-------------------|---------------------------|
| head + body | <i>C. albellus</i> vs. <i>C. alpinus</i> (a)  | <163.5mm   | 1: PreA/LJ *    | 6.33-7.44       | 9.24-9.97       | 27.13             | 0.04                      |
|             |   |            | 2: AFae/M       | 1.65-2.25       | 2.58-2.63       | 25.94             | 0.04                      |
| body        | <i>C. albellus</i> vs. <i>C. alpinus</i>      | <163.5mm   | 1: PecF2/DFAd * | 0.81-1.06       | 0.78-0.8        | 9.97              | 0.14                      |
|             |   |            | 2: DHL/PreD     | 0.34-0.42       | 0.32-0.34       | 9.4               | 0.15                      |
| head        | <i>C. albellus</i> vs. <i>C. alpinus</i>      | <163.5mm   | 1: HD/LJ        | 1.30-1.55       | 1.77-1.92       | 15.43             | 0.02                      |
|             |   |            | 2: IOW/UJW      | 0.89-1.30       | 1.20-1.26       | 14.14             | 0.02                      |
| head + body | <i>C. albellus</i> vs. <i>C. fatioi</i>       | <163.5mm   | 1: PecF2/PreA * | 0.22-0.28       | 0.2-0.22        | 5.78              | 0.16                      |
|             |   |            | 2: DHL/PreP     | 0.31-0.38       | 0.30-0.32       | 4.49              | 0.2                       |
| body        | <i>C. albellus</i> vs. <i>C. fatioi</i>       | <163.5mm   | 1: PecF2/PreA * | 0.22-0.28       | 0.2-0.22        | 6.76              | 0.17                      |
|             |   |            | 2: DHL/TL       | 0.13-0.18       | 0.13-0.14       | 5.7               | 0.19                      |
| head        | <i>C. albellus</i> vs. <i>C. fatioi</i>       | <163.5mm   | 1: UJ/ES *      | 6.81-12.42      | 4.51-6.15       | 8.63              | 0.12                      |
|             |   |            | 2: EH/HL *      | 0.27-0.31       | 0.23-0.27       | 7.3               | 0.14                      |
| head + body | <i>C. albellus</i> vs. <i>C. brienzii</i> (b) | <163.5mm   | 1: PreD/LJ *    | 3.99-4.68       | 5.05-5.57       | 47.9              | 0.01                      |
|             |   |            | 2: M/ES *       | 5.35-9.76       | 3.31-4.37       | 47.63             | 0.01                      |
| body        | <i>C. albellus</i> vs. <i>C. brienzii</i>     | <163.5mm   | 1: PecF2/PreD * | 0.36-0.45       | 0.29-0.32       | 15.95             | 0.06                      |
|             |   |            | 2: DHL/TL       | 0.13-0.18       | 0.13-0.14       | 9.91              | 0.05                      |
| head        | <i>C. albellus</i> vs. <i>C. brienzii</i>     | <163.5mm   | 1: LJ/ES *      | 9.62-17.28      | 6.01-6.49       | 12.51             | 0.05                      |
|             |   |            | 2: HL/UJ        | 2.87-3.5        | 3.19-3.6        | 8.87              | 0.04                      |
| Characters  | Species comparison                            | Size range | Best ratios     | Range species 1 | Range species 2 | Standard distance | $\delta$ (Shape vs. size) |
| head + body | <i>C. alpinus</i> vs. <i>C. fatioi</i> (b)    | >163.5mm   | 1: AFae/UJ *    | 1.96-2.5        | 1.66-1.96       | 26.08             | 0.04                      |
|             |   |            | 2: CL/PreA      | 0.14-0.18       | 0.17-0.21       | 26.46             | 0.04                      |
| body        | <i>C. alpinus</i> vs. <i>C. fatioi</i>        | >163.5mm   | 1: AFae/TL      | 0.1-0.11        | 0.09-0.1        | 13.41             | 0.11                      |
|             |   |            | 2: CL/PreA      | 0.14-0.18       | 0.17-0.21       | 13.41             | 0.11                      |
| head        | <i>C. alpinus</i> vs. <i>C. fatioi</i>        | >163.5mm   | 1: HL/UJ *      | 3.55-3.93       | 3.13-3.55       | 11.51             | 0.07                      |
|             |   |            | 2: LJW/UJW      | 0.33-0.44       | 0.38-0.55       | 11.02             | 0.07                      |
| head + body | <i>C. alpinus</i> vs. <i>C. brienzii</i> (c)  | >163.5mm   | 1: CD/SW *      | 2.25-2.64       | 1.82-2.04       | 34.25             | 0.02                      |
|             |   |            | 2: LJW/UJW *    | 0.33-0.44       | 0.45-0.55       | 33.91             | 0.02                      |
| body        | <i>C. alpinus</i> vs. <i>C. brienzii</i> (d)  | >163.5mm   | 1: DFAe/PAdC *  | 1.11-1.32       | 0.96-1.16       | 18.53             | 0.07                      |
|             |   |            | 2: CD/AFB       | 0.61-0.68       | 0.52-0.62       | 18.31             | 0.07                      |
| head        | <i>C. alpinus</i> vs. <i>C. brienzii</i> (e)  | >163.5mm   | 1: LJW/UJW *    | 0.33-0.44       | 0.45-0.55       | 7.44              | 0.08                      |
|             |   |            | 2: PostO/UJ     | 1.8-2.12        | 1.57-1.86       | 6.78              | 0.08                      |
| Characters  | Species comparison                            | Size range | Best ratios     | Range species 1 | Range species 2 | Standard distance | $\delta$ (Shape vs. size) |
| head + body | <i>C. fatioi</i> vs. <i>C. brienzii</i> (f)   | >163.5mm   | 1: CL/PAdC      | 0.71-0.86       | 0.66-0.76       | 7.46              | 0.08                      |
|             |   |            | 2: BD/LJ        | 2.44-3.05       | 2.31-2.82       | 7.36              | 0.08                      |
| body        | <i>C. fatioi</i> vs. <i>C. brienzii</i>       | >163.5mm   | 1: CL/PAdC      | 0.71-0.86       | 0.66-0.76       | 6.04              | 0.1                       |
|             |   |            | 2: CF/BD        | 0.87-1.13       | 0.93-1.12       | 5.92              | 0.1                       |
| head        | <i>C. fatioi</i> vs. <i>C. brienzii</i>       | >163.5mm   | 1: ED/M         | 1.03-1.19       | 1.04-1.57       | 3.58              | 0.18                      |
|             |   |            | 2: HW/UJW       | 1.89-2.23       | 1.88-2.33       | 3.38              | 0.19                      |
| Characters  | Species comparison                            | Size range | Best ratios     | Range species 1 | Range species 2 | Standard distance | $\delta$ (Shape vs. size) |
| head + body | <i>C. alpinus</i> vs. other 3 species         | <163.5mm   | 1: DFAe/LJ *    | 2.57-2.58       | 1.6-2.1         | 23.47             | 0.03                      |
|             |   |            | 2: AdFB/PAdC    | 0.26-0.28       | 0.21-0.42       | 22.66             | 0.03                      |

| Characters  | Species comparison  | Size range | Best ratios     | Range species 1    | Range species 2 | Standard distance | $\delta$ (Shape vs. size) |
|-------------|---|------------|-----------------|--------------------|-----------------|-------------------|---------------------------|
| head + body | <i>C. albellus</i> vs. <i>other 3 species</i>                   | <163.5mm   | 1: PostD/EH *   | 5.47-6.93          | 7.5-8.9         | 48.36             | 0.02                      |
|             |   |            | 2: UJW/ES       | 4.88-9.3           | 3.41-5.31       | 48.13             | 0.02                      |
| head + body | <i>C. alpinus</i> vs. <i>C. fatioi</i> + <i>C. brienzii</i> (g) | >163.5mm   | 1: DFAe/UJ *    | 3.28-4.1           | 2.58-3.19       | 24.71             | 0.05                      |
|             |   |            | 2: CD/SW *      | 2.25-2.64          | 1.76-2.27       | 24.37             | 0.05                      |
| Characters  | Species comparison  | Size range | Best ratios     | Range species 1    | Range species 2 | Standard distance | $\delta$ (Shape vs. size) |
| head + body | <i>C. albellus</i> vs. <i>C. alpinus</i> (h)                    | 100-290    | 1: PreD/LJ *    | 3.99-4.68          | 5.6-6.81        | 22.86             | 0.13                      |
|             |   |            | 2: DFAe/UJ *    | 2.14-2.79          | 3.25-4.1        | 21.65             | 0.14                      |
| head        | <i>C. albellus</i> vs. <i>C. alpinus</i>                        | 100-290    | 1: HD/UJ *      | 1.87-2.2           | 2.38-2.78       | 14.39             | 0.18                      |
| head + body | <i>C. albellus</i> vs. <i>C. fatioi</i>                         | 100-290    | 2: LJ/IOW *     | 1.53-1.99          | 1.33-1.57       | 13.25             | 0.19                      |
|             |   |            | 1: PreP/EH *    | 6.56-7.98          | 8.94-11.43      | 15.95             | 0.13                      |
| head + body | <i>C. albellus</i> vs. <i>C. fatioi</i>                         | 100-290    | 2: CL/UJ        | 1.44-2.02          | 1.93-2.72       | 15.09             | 0.14                      |
|             |   |            | 1: PreD/EH *    | 6.1-7.58           | 8.12-10.32      | 50.86             | 0.04                      |
| head + body | <i>C. albellus</i> vs. <i>C. brienzii</i> (i)                   | 100-290    | 2: CL/LJ        | 0.99-1.45          | 1.38-1.65       | 50.6              | 0.04                      |
|             |   |            | 1: EH/HL *      | 0.27-0.31          | 0.22-0.27       | 9.33              | 0.18                      |
| head        | <i>C. albellus</i> vs. <i>C. brienzii</i>                       | 100-290    | 2: Lj/ES        | 9.62-17.28         | 6.08-12.43      | 8.57              | 0.22                      |
| Characters  | Species comparison  | Size range | Best ratios     | Range species 1    | Range species 2 | Standard distance | $\delta$ (Shape vs. size) |
| head + body | <i>C. alpinus</i> vs. <i>C. brienzii</i> (j)                    | 100-290    | 1: DFAd/LJW *   | 9.84-14.82         | 6.05-8.91       | 20.72             | 0.03                      |
|             |   |            | 2: DHL/LJ *     | 1.84-2.22          | 1.63-1.82       | 20.47             | 0.02                      |
| body        | <i>C. alpinus</i> vs. <i>C. brienzii</i> (k)                    | 100-290    | 1: PecF2/DFAd * | 0.74-0.85          | 0.85-1.03       | 87.52             | <0.01                     |
|             |   |            | 2: CD/PostD     | 0.17-0.2           | 0.15-0.18       | 87.48             | <0.01                     |
| head        | <i>C. alpinus</i> vs. <i>C. brienzii</i>                        | 100-290    | 1: HD/LJW *     | 6.72-9.39          | 5.23-6.66       | 11.94             | 0.04                      |
| head + body | <i>C. alpinus</i> vs. <i>C. fatioi</i> (h)                      | 100-290    | 2: HL/LJ *      | 2.54-2.96          | 2.19-2.47       | 11.61             | 0.04                      |
|             |   |            | 1: DFAe/UJ *    | 3.25-4.1           | 2.45-3.17       | 18.98             | 0.03                      |
| body        | <i>C. alpinus</i> vs. <i>C. fatioi</i>                          | 100-290    | 2: PecF2/AFAe   | 1.24-1.47          | 1.37-1.63       | 18.63             | 0.03                      |
|             |   |            | 1: PecF2/DFAd * | 0.77-0.89          | 0.87-1.02       | 9.25              | 0.08                      |
| head        | <i>C. alpinus</i> vs. <i>C. fatioi</i>                          | 100-290    | 2: AFAe/PostD   | 0.27-0.32          | 0.22-0.29       | 8.71              | 0.08                      |
|             |   |            | 1: LJW/UJW      | 0.33-0.47          | 0.37-0.55       | 5.62              | 0.08                      |
| head        | <i>C. alpinus</i> vs. <i>C. fatioi</i>                          | 100-290    | 2: HL/UJ        | 3.43-3.93          | 3.13-3.63       | 4.98              | 0.08                      |
|             |   |            | Characters      | Species comparison | Size range      | Best ratios       | Range species 1           |
| head + body | <i>C. fatioi</i> vs. <i>C. brienzii</i> (l)                     | 100-290    | 1: AFB/BD       | 0.45-0.67          | 0.44-0.58       | 28.19             | <0.01                     |
|             |   |            | 2: PreD/M       | 8.87-14.85         | 9.13-11.41      | 28.16             | <0.01                     |
| body        | <i>C. fatioi</i> vs. <i>C. brienzii</i>                         | 100-290    | 1: AFB/BD       | 0.45-0.67          | 0.44-0.58       | 2.76              | 0.05                      |
|             |   |            | 2: PreP/PreA    | 0.58-0.65          | 0.57-0.64       | 2.51              | 0.05                      |
| head        | <i>C. fatioi</i> vs. <i>C. brienzii</i>                         | 100-290    | 1: ED/M         | 1.04-1.57          | 1.03-1.28       | 1.72              | 0.1                       |
|             |   |            | 2: SN/MW        | 2.09-2.63          | 1.78-2.87       | 1.52              | 0.1                       |
| Characters  | Species comparison  | Size range | Best ratios     | Range species 1    | Range species 2 | Standard distance | $\delta$ (Shape vs. size) |
| head + body | <i>C. albellus</i> vs. <i>other 3 species</i>                   | 100-290    | 1: PreD/EH *    | 6.1-7.58           | 8.12-10.5       | 10.89             | 0.16                      |
|             |   |            | 2: CL/UJ        | 1.44-2.02          | 1.85-2.72       | 9.79              | 0.17                      |
| head + body | <i>C. alpinus</i> vs. <i>other 3 species</i>                    | 100-290    | 1: DFAe/UJ *    | 3.25-4.1           | 2.14-3.19       | 9.59              | 0.11                      |
| body        | <i>C. alpinus</i> vs. <i>other 3 species</i>                    | 100-290    | 2: LJW/UJW      | 0.33-0.47          | 0.34-0.55       | 8.98              | 0.12                      |

(a) PelvS, PecF1, DFAd, DFAe, DFPe, TL, SL, EH, SD, SW, INW, IOW

(b) PelvFS, PelvFB, PecFB, DFPe, TL, EH, ED, SD, IOW

(c) PelvFB, PelvFS, PelvE, PecF1, DFB, DFAe, DFPe, AFB, AFAe, AdFB, CF, PAdC, PreP, PreA, SL, TL, BD, PostD, DHL, ED, EH, ES, PostO, HD, MW, SN, SD, SW, IOW, INW

(d) PecFB, PelvFB, PelvF, PelvFS, PecF1, DFAe, DFPe, AFAe, AdFB, PreP, CF, TL, PostD

(e) ED, EH, HD, SD, SW, INW

(f) PelvFB, PelvFS, PelvE, PecFB, DFAe, DFAd, DFPe, CF, PreP, SL, TL, ED, EH, MW, SD, SW, IOW, INW, ES

(g) PelvFS, PecF1, PecFB, DFAd, DFPe, SL, TL, ED, EH, INW, CF

(h) PelvS, PecF1, DFAd, DFAe, DFPe, TL, SL, EH, SD, SW, INW, IOW

(i) PelvFS

(j) PelvFB, PelvFS, PelvF, PecF1, DFAe, DFPe, AFB, AFAe, CF, SL, TL, BD, ED, EH, ES, PostO, HD, MW, SN, SD, SW, IOW, INW

(k) PelvFS, PecF1, CF, SL, TL

(l) PelvS, TL, INW

**Distribution and notes on biology.** *Coregonus macrophthalmus* is found in Lake Constance, especially in the upper basin (Obersee). It is unclear if it also occurs in the lower basin (Untersee) of the lake.

**Common name.** Gangfisch.

**Table 12.** Morphological and meristic data of *C. gutturosus* Gmelin, 1818, *C. arenicolus* Kottelat, 1997, *C. macrophthalmus* Nüsslin, 1882 and *C. wartmanni* Bloch, 1784 from Lake Constance. *Coregonus gutturosus* Gmelin, 1818, non-types N = 10. *Coregonus arenicolus* Kottelat, 1997, holotype, NMBE-1076223 (Eawag-239-1), sex unknown; paratypes N = 3. *Coregonus macrophthalmus* Nüsslin, 1882, syntypes N = 7. *C. wartmanni* Bloch, 1784, non-type, NMBE-1076206, female.

| Morphological characters      | <i>C. gutturosus</i> |            |               | <i>C. arenicolus</i> |            |            | <i>C. macrophthalmus</i> |            |            | <i>C. wartmanni</i> |         |
|-------------------------------|----------------------|------------|---------------|----------------------|------------|------------|--------------------------|------------|------------|---------------------|---------|
|                               | Non-types (N=10)     |            | Holotype      | Paratypes (N=3)      |            | N-total    | Synatypes (N=7)          |            | N-total    | Non-type            |         |
|                               | N-total              | Mean±StDev |               | Range                | Mean±StDev |            | Range                    | Mean±StDev |            | Range               | N-total |
| SL (mm)                       | 10                   | 220.4±36.8 | (169–292)     | 296.0                | 3          | 301.3±12.5 | (289–314)                | 7          | 213.9±12.4 | (193–235)           | 301     |
| Percentage of standard length |                      |            |               |                      |            |            |                          |            |            |                     |         |
| PelvFB                        | 10                   | 4.1±0.2    | (3.7–4.4)     | 3.9                  | 3          | 4.4±0.3    | (3.9–4.6)                | 7          | 3.8±0.3    | (3.3–4.2)           | 3.8     |
| PelvFS                        | 10                   | 6.1±0.4    | (5.3–6.7)     | 5.4                  | 3          | 5.7±0.5    | (5.2–6.1)                | 7          | 5.7±0.7    | (4.8–6.9)           | 6.5     |
| PelvF                         | 10                   | 17.1±1.2   | (15.4–19.1)   | 17.3                 | 3          | 17.3±0.7   | (16.8–18.1)              | 7          | 16.5±0.9   | (15.2–17.6)         | 15.4    |
| PrecFB                        | 10                   | 3.4±0.3    | (2.9–3.9)     | 3.3                  | 3          | 3.4±0.2    | (3.2–3.5)                | 7          | 3.2±0.4    | (2.8–3.9)           | 3       |
| PrecF1                        | 10                   | 16.8±1.1   | (14.8–18.9)   | 14.4                 | 3          | 16.8±0.5   | (14.4–17.2)              | 7          | 16.4±1.2   | (15.1–18.1)         | 16      |
| PrecF2                        | 10                   | 18.2±1.5   | (16.8–20.3)   | 15.7                 | 3          | 17.4±0.8   | (15.7–18)                | 7          | 17.1±1     | (15.6–18.4)         | 17      |
| DfB                           | 10                   | 11.9±0.7   | (10.7–12.8)   | 12.2                 | 3          | 12.2±1.1   | (11.0–13.1)              | 7          | 11.6±0.7   | (10.8–12.4)         | 11.2    |
| DfAe                          | 10                   | 19.3±1.3   | (17.6–21.6)   | 18.9                 | 3          | 19.2±1.2   | (18.0–20.3)              | 7          | 18.2±1.2   | (16.6–19.6)         | 16.6    |
| DfAd                          | 10                   | 20.4±1.1   | (19.0–22.2)   | 20.2                 | 3          | 20.5±1.3   | (19.3–21.9)              | 7          | 19.2±1.3   | (17.2–20.5)         | 18.2    |
| DfPe                          | 10                   | 5.5±0.7    | (4.8–7.0)     | 5.2                  | 3          | 5.5±0.2    | (5.2–5.7)                | 7          | 5.2±0.6    | (4.4–5.9)           | 4.6     |
| AfB                           | 10                   | 12.4±0.8   | (11.4–13.4)   | 11.9                 | 3          | 11.5±1.1   | (10.7–12.7)              | 7          | 12.3±1.3   | (10.6–14.2)         | 12.5    |
| AfAe                          | 10                   | 12.3±1.0   | (10.7–13.9)   | 13.2                 | 3          | 13.3±0.5   | (12.9–13.8)              | 5          | 12.1±1.3   | (10.8–13.9)         | 11.1    |
| AdfB                          | 10                   | 5.6±0.4    | (4.9–6.1)     | 5.7                  | 3          | 5.0±1.3    | (3.7–6.2)                | 7          | 5.3±0.3    | (4.9–5.8)           | 4       |
| Cf                            | 9                    | 23.2±1.9   | (20.8–25.6)   | na                   | 2          | 24±0.1     | (24–24.1)                | 3          | 22.6±1.2   | (21.8–24)           | 23.8    |
| Cd                            | 10                   | 7.4±0.4    | (6.7–8.2)     | 7.7                  | 3          | 8.1±0.1    | (7.7–8.2)                | 7          | 7.4±0.4    | (6.9–8)             | 7.4     |
| Cl                            | 10                   | 12.9±0.8   | (11.5–13.9)   | 14.4                 | 3          | 12.9±0.8   | (12.0–14.4)              | 7          | 13.8±1.3   | (12.4–16.5)         | 13.2    |
| PAdC                          | 10                   | 18.5±0.6   | (17.4–19.3)   | 19.6                 | 3          | 17.2±2.2   | (14.6–19.6)              | 7          | 18.9±1.1   | (17.6–20.2)         | 17.8    |
| DHL                           | 10                   | 16.8±0.8   | (15.4–18.1)   | 15.1                 | 3          | 15.1±0.2   | (14.8–15.3)              | 7          | 15.7±0.8   | (14.4–16.5)         | 14.5    |
| PreP                          | 10                   | 52.7±1.4   | (50.4–54.1)   | 49.5                 | 3          | 50.6±0.5   | (49.5–51.0)              | 7          | 51.7±1.7   | (48.1–53.1)         | 50.7    |
| PreA                          | 10                   | 77.9±1.4   | (76.0–80.4)   | 75.0                 | 3          | 79.2±0.9   | (75.0–80.3)              | 7          | 76.8±0.9   | (75.7–78.3)         | 77.4    |
| PreD                          | 10                   | 48.4±0.9   | (46.8–49.6)   | 47.9                 | 3          | 49.2±0.5   | (47.9–49.6)              | 7          | 47±1       | (45.8–48.5)         | 47.3    |
| BD                            | 10                   | 25.9±1.9   | (22.9–29.6)   | 24.4                 | 3          | 26.2±0.8   | (24.4–27.1)              | 7          | 23.5±1.9   | (21.0–26.9)         | 23.5    |
| PostD                         | 10                   | 43±1.5     | (40.6–45.4)   | 44.8                 | 3          | 42.2±1.7   | (40.4–44.8)              | 7          | 43±1.4     | (41.6–45.7)         | 44      |
| Tl                            | 9                    | 120.2±3    | (115.1–124.3) | na                   | 2          | 121.5±2.9  | (119.4–123.5)            | 3          | 119.2±0.7  | (118.9–120)         | 120.6   |
| Hl (mm)                       | 10                   | 50.3±7.1   | (41.6–62.4)   | 61.8                 | 3          | 63.7±3.9   | (59.6–67.2)              | 7          | 47.5±3.2   | (42.6–51.3)         | 64.7    |
| Percentage of head length     |                      |            |               |                      |            |            |                          |            |            |                     |         |
| SN                            | 10                   | 22.4±0.7   | (21.1–23.1)   | 23.4                 | 3          | 23.4±1.6   | (21.6–24.6)              | 7          | 21.7±2.7   | (18–25.6)           | 24      |
| ED                            | 10                   | 21.1±1.4   | (19.4–23)     | 19.6                 | 3          | 17.7±0.4   | (17.3–19.6)              | 7          | 24.1±1.7   | (21.3–26.1)         | 18.9    |
| EC                            | 10                   | 26.9±1.2   | (25.4–29.3)   | 25.7                 | 3          | 25±0.8     | (24.1–25.7)              | 7          | 28.9±2     | (25.4–30.8)         | 23.9    |
| EH                            | 10                   | 21.3±0.6   | (20.5–22.6)   | 20.8                 | 3          | 19.6±0.9   | (18.8–20.8)              | 7          | 23.2±2.1   | (19.5–25.6)         | 19      |

| Morphological characters | <i>C. guttirostris</i> (N=10) |                  |             | <i>C. arenicolus</i> |                 |          | <i>C. macrophthalminus</i> |                |          | <i>C. waarmanni</i><br>Non-type |      |         |
|--------------------------|-------------------------------|------------------|-------------|----------------------|-----------------|----------|----------------------------|----------------|----------|---------------------------------|------|---------|
|                          | N-total                       | Non-types (N=10) |             | N-total              | Paratypes (N=3) |          | N-total                    | Syntypes (N=7) |          |                                 |      |         |
|                          |                               | Mean±StdDev      | Range       |                      | Mean±StdDev     | Range    |                            | Mean±StdDev    | Range    |                                 |      |         |
| ES                       | 10                            | 4.8±0.7          | (3.5–5.6)   | 4.9                  | 3               | 5.2±0.5  | (4.6–5.5)                  | 7              | 3.9±0.8  | (2.7–4.6)                       | 5.1  |         |
| PostO                    | 10                            | 52.8±1           | (51.5–54.4) | 55.7                 | 3               | 54±1     | (53–55.7)                  | 7              | 50.2±1.9 | (48.5–53.2)                     | 53.4 |         |
| HD                       | 10                            | 74.2±3.2         | (69.9–80.6) | 68.2                 | 3               | 72.6±3   | (68.2–75)                  | 7              | 68.6±4.8 | (61.6–76.3)                     | 67.6 |         |
| MW                       | 10                            | 9.8±0.6          | (9–11.2)    | 10.4                 | 3               | 10.5±0.5 | (10–11)                    | 6              | 10.1±0.8 | (8.7–11.1)                      | 10.6 |         |
| UJ                       | 10                            | 26.8±1.2         | (24.6–29)   | 27.2                 | 3               | 29.3±1   | (27.2–30.1)                | 7              | 30.3±2.3 | (26.7–33.8)                     | 28.8 |         |
| LJ                       | 10                            | 36.6±1.4         | (34.3–39.1) | 37.8                 | 3               | 38.7±0.6 | (37.8–39.1)                | 7              | 42.2±2   | (40–44.4)                       | 43.5 |         |
| M                        | 10                            | 18.9±1.3         | (17.3–21.7) | 21.1                 | 3               | 19.7±0.9 | (18.6–21.1)                | 5              | 23.1±1.9 | (20.1–24.7)                     | 22   |         |
| SD                       | 10                            | 10.2±0.8         | (9.3–11.9)  | 9.7                  | 3               | 10.9±1.3 | (9.7–12.3)                 | 7              | 7.4±1.2  | (5.5–9.5)                       | 6.8  |         |
| SW                       | 10                            | 15.1±1.6         | (12.3–17.6) | 14.9                 | 3               | 14.3±0.7 | (14.3–18.5)                | 7              | 15.6±1.2 | (14.1–17.4)                     | 15   |         |
| HW                       | 10                            | 56.1±4.3         | (46.7–62.3) | 51.8                 | 3               | 50.8±0.5 | (50.5–51.8)                | 7              | 41.6±1.5 | (39.3–43.3)                     | 45.5 |         |
| IOW                      | 10                            | 28.4±1.7         | (26.2–31.6) | 29.6                 | 3               | 29.7±1   | (28.8–30.8)                | 7              | 26.1±1.6 | (23.8–28.9)                     | 24.2 |         |
| INW                      | 10                            | 11.9±0.7         | (10.7–12.7) | 12.0                 | 3               | 13.7±0.1 | (12–13.8)                  | 5              | 11.9±1.3 | (10.7–14.1)                     | 12.7 |         |
| LJW                      | 10                            | 7.7±1            | (6.8–9.9)   | 7.8                  | 3               | 8.1±0.3  | (7.8–8.5)                  | 5              | 7.8±1    | (6.4–8.8)                       | 8.1  |         |
| UJW                      | 10                            | 25.2±1.2         | (23.1–26.8) | 24.9                 | 3               | 26.4±0.8 | (24.9–27.2)                | 7              | 21.6±1.9 | (18.6–24.6)                     | 22.7 |         |
| MGR                      | 9                             | 6.9±1.3          | (4.1–8.7)   | 9.9                  | 2               | 10.2±0.6 | (9.8–10.6)                 | 4              | 12.5±1.4 | (11.6–14.7)                     | 10.8 |         |
| LGR                      | 9                             | 8.2±1.4          | (6.7–10.6)  | 10.9                 | 2               | 11.5±0.6 | (10.9–12)                  | 4              | 14.6±1.2 | (13.3–16.1)                     | 11.3 |         |
| UA                       | na                            | na               | na          | na                   | na              | na       | na                         | na             | na       | na                              | na   |         |
| LA                       | na                            | na               | na          | na                   | na              | na       | na                         | na             | na       | na                              | na   |         |
| Meristic character       | N-total                       | Mode             | Range       | N-total              | Mode            | Range    | N-total                    | Mode           | Range    | N-total                         | Mode | Range   |
| PelvF unbranched         | 10                            | 1                | (1–1)       | 3                    | 1               | (1–1)    | 7                          | 1              | (1–1)    | 1                               | 1    | (1–1)   |
| PelvF branched           | 10                            | 11               | (9–11)      | 3                    | 11              | (11–11)  | 7                          | 10             | (10–11)  | 12                              | 10   | (10–11) |
| PecF unbranched          | 10                            | 1                | (1–1)       | 3                    | 1               | (1–1)    | 7                          | 1              | (1–1)    | 1                               | 1    | (1–1)   |
| PecF branched            | 10                            | 13               | (12–14)     | 3                    | 12              | (12–14)  | 7                          | 15             | (14–15)  | 16                              | 15   | (14–15) |
| DF unbranched            | 10                            | 4                | (3–4)       | 3                    | 4               | (4–4)    | 7                          | 4              | (4–4)    | 4                               | 4    | (4–4)   |
| DF branched              | 10                            | 10               | (9–10)      | 3                    | 10              | (9–10)   | 7                          | 9              | (9–10)   | 10                              | 9    | (9–10)  |
| AF unbranched            | 10                            | 3                | (3–4)       | 3                    | 3               | (3–3)    | 7                          | 3              | (3–3)    | 4                               | 3    | (3–4)   |
| AF branched              | 10                            | 11               | (10–12)     | 3                    | 10              | (10–11)  | 7                          | 11             | (10–13)  | 13                              | 11   | (10–13) |
| LS                       | 10                            | 78               | (76–82)     | 82                   | na              | (82–90)  | 7                          | 80             | (73–80)  | 84                              | 80   | (73–80) |
| PDS                      | 10                            | 33               | (31–35)     | 36                   | na              | (36–44)  | 7                          | 32             | (32–36)  | 34                              | 32   | (32–36) |
| TDS                      | 10                            | 10               | (9–10)      | 10                   | 10              | (10–11)  | 7                          | 9              | (9–10)   | 10                              | 9    | (9–10)  |
| TAS                      | 10                            | 8                | (7–9)       | 8                    | 3               | (8–9)    | 7                          | 7              | (7–9)    | 8                               | 7    | (7–9)   |
| TPS                      | 10                            | 8                | (8–9)       | 8                    | 9               | (8–9)    | 7                          | 9              | (8–9)    | 8                               | 7    | (7–9)   |
| UGR                      | 9                             | 7                | (7–9)       | 9                    | na              | (9–12)   | 4                          | 14             | (12–14)  | 11                              | 14   | (12–14) |
| LGR                      | 9                             | 10               | (9–12)      | 13                   | na              | (13–19)  | 4                          | 24             | (22–24)  | 23                              | 24   | (22–24) |
| total GR                 | 9                             | 19               | (16–21)     | 22                   | na              | (22–31)  | 4                          | 36             | (36–38)  | 34                              | 36   | (36–38) |

***Coregonus wartmanni*, Bloch, 1784****Figure 11**

**Material examined.** *Non-type*. NMBE-1076206, Switzerland, Lake Constance (47°38'N, 9°22'E), 301 mm SL, sex female.

**Distribution and notes on biology.** *Coregonus wartmanni* is found in Lake Constance, especially in the upper basin (Obersee). It is unclear if it also occurs in the lower basin (Untersee).

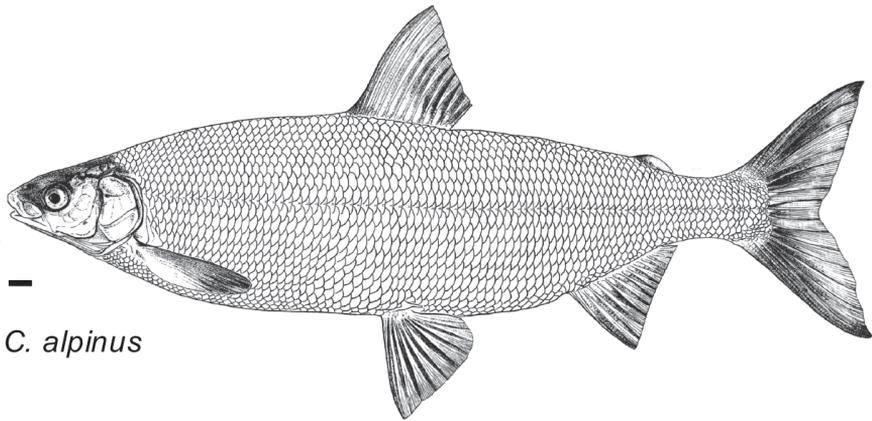
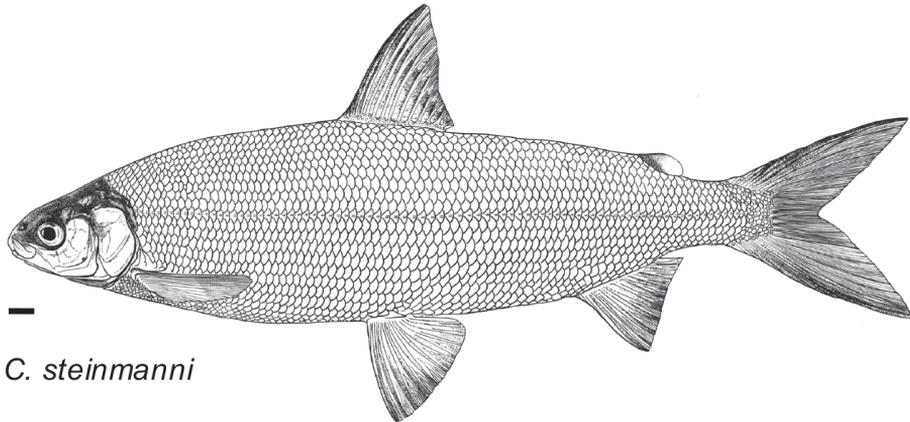
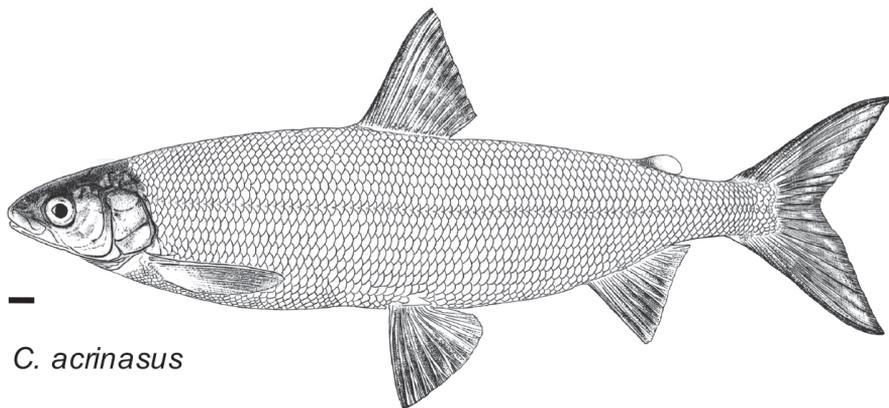
**Common name.** Blaufelchen.

**Identification key to the species of lakes Thun and Brienz****Lake Thun**

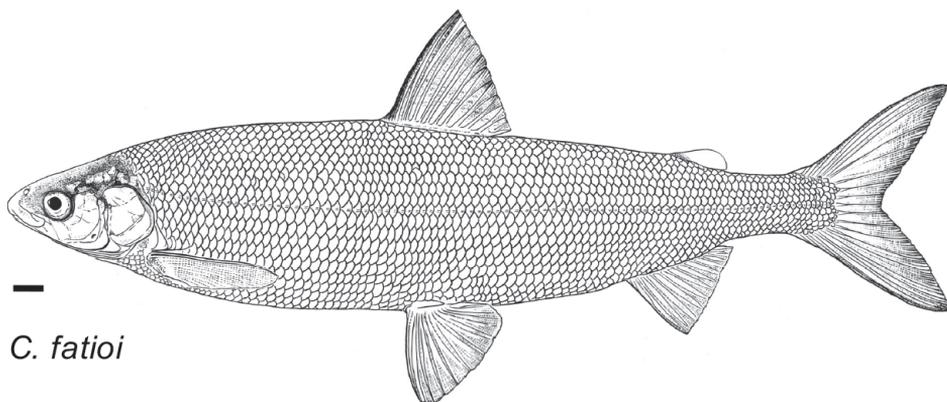
- 1 Caudal peduncle depth / upper jaw length ratio is 1.36–1.65 and caudal peduncle depth / maxilla length ratio is 1.77–2.24 ..... 2
- Caudal peduncle depth / upper jaw length ratio is 0.96–1.43 ..... 3
- 2 Total number of gill rakers 25–30 ..... *C. alpinus*
- Total number of gill rakers 31–35 ..... *C. steinmanni*
- 3 Total number of gill rakers 15–27 ..... *C. profundus*
- Total number of gill rakers 30–44 ..... 4
- 4 Colouration above the lateral line on the dorsum from a pale rose colouration to a pale brown colouration; no or few small pigmented dots on the edge of the scales or on the boundary of two scales on the flank; no pigmented dots on the dorsum ..... *C. albellus*
- Colouration above the lateral line on the dorsum from a light to dark green and rarely a light olive; moderate to many dots on the edge of the scales or on the boundary of two scales on the flank and/or the dorsum ..... 5
- 5 Angle to body axis of the erected dorsal fin approx. 60–80° ..... *C. fatioi*
- Angle to body axis of the erected dorsal fin approx. 40–60° ..... *C. acrinus*

**Lake Brienz**

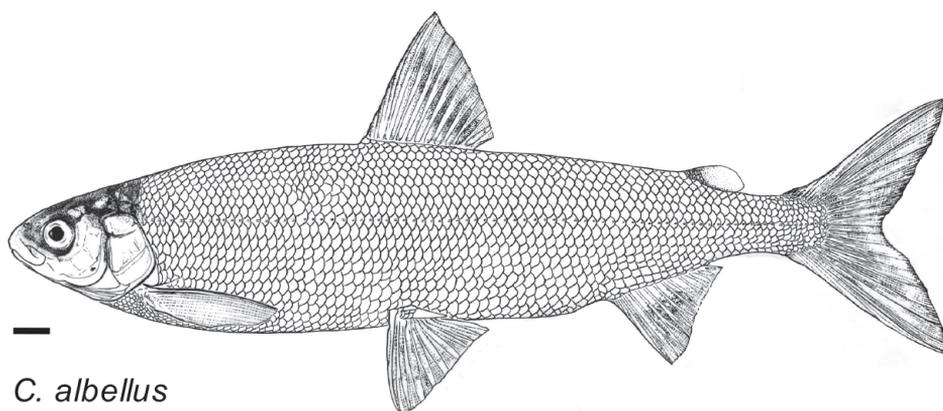
- 1 Total number of gill rakers 26–30 and erected dorsal fin length / upper jaw length ratio is 3.25–4.1 ..... *C. alpinus*
- Total number of gill rakers 32–42 and erected dorsal fin length / upper jaw length ratio is 2.14–3.19 ..... 2
- 2 Predorsal length / eye height ratio is 6.1–7.58 ..... *C. albellus*
- Predorsal length / eye height ratio is 8.12–10.5 ..... 3
- 3 Body depth 19.6–25.1% SL, eye depth 23.1–28.3 % HL ..... *C. brienzii*
- Body depth 22.1–26.2% SL, eye depth 21.2–27.6% HL ..... *C. fatioi*

*C. alpinus**C. steinmanni**C. acrinus*

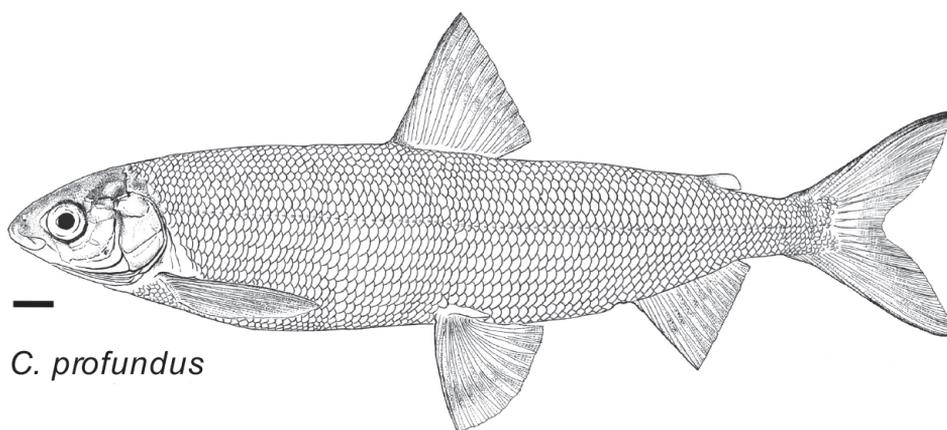
**Figure 12.** Illustrations of specimens of each species from Lake Thun. From top to bottom: *Coregonus alpinus*: non-type, NMBE-1077244, 343 mm, male; *Coregonus steinmanni*: paratype, NMBE-1077218, 289.5 mm, male; *Coregonus acrinus*: paratype, NMBE-1077270, 270 mm, male; *Coregonus fatioi*: non-type, NMBE-1077138, 267 mm, male; *Coregonus albellus*: non-type, NMBE-1077188, 215 mm, male; *Coregonus profundus*: non-type, Eawag-123850, 195 mm, male. The black scale (1 cm) below each fish acts as a reference for the actual size of the specimen.



*C. fatioi*



*C. albellus*



*C. profundus*

**Figure 12.** Continued.

## Discussion

Phylogeographic studies have shown that the pre-alpine whitefish are a monophyletic clade, most closely related to whitefish from northern Europe. The clade is of hybrid origin involving two glacial lineages that must have come into secondary contact several hundred thousand years after their separation. Independent events of intra-lacustrine speciation led to a series of adaptive radiations in each major lake system of the northern pre-Alps (Hudson et al. 2011). Up to six endemic species can be found in the most diverse of these adaptive radiations (Vonlanthen et al. 2012; Hudson et al. 2016; Dönz et al. 2018). Here we take an integrative taxonomic approach, combining genetic assignments (Dönz et al. 2018) with morphological and meristic traits and multivariate statistical methods to delineate species and revise the taxonomy of the whitefish radiation of lakes Thun and Brienz in the western Aare catchment of Switzerland. We distinguish and characterize seven whitefish species from these lakes. Three of them occur in both lakes and three may be unique to Lake Thun and one may be unique to Lake Brienz. The three species that occur in both lakes have been described more than 130 years ago. Two of these species, *C. alpinus* and *C. albellus*, were described by Fatio (1885 and 1890 respectively). The third species, *C. fatioi*, was renamed by Kottelat (1997), but first described by Fatio (1890). Kottelat (1997) proposed *C. fatioi* as a replacement name, since the name given by Fatio (1890) was preoccupied by another species described by Fatio (1885). Our own earlier research combining genetics and ecology had shown that a fourth species is present in both lakes (Dönz et al. 2018). However, recent whole-genome data (De-Kayne et al. unpublished) suggest that this newly discovered species is genetically different between lakes. We thus describe this species here as *Coregonus steinmanni* sp. nov. for the specimens from Lake Thun and those from Lake Brienz we designate as *C. brienzi*. Our earlier research (Hudson et al. 2011; Vonlanthen et al. 2012; Dönz et al. 2018) had further revealed that Lake Thun harbours two additional undescribed species and we describe these here as *Coregonus profundus* sp. nov. and *Coregonus acrinasus* sp. nov. Consistent with previous work (Dönz et al. 2018), recent genomic analyses (whole-genome data: De-Kayne et al. unpublished) find that the three species, *C. alpinus*, *C. fatioi* and *C. albellus*, occurring in both lakes cluster by species, whereas *C. steinmanni* from Lake Thun and *C. brienzi* from Lake Brienz (formerly *C. steinmanni* from Lake Brienz; Dönz et al. 2018) are not each others closest relatives. Interestingly, we also find morphological relationships to differ between the lakes; in Lake Thun *C. steinmanni* groups in morphospace with *C. alpinus*, whereas in Lake Brienz *C. brienzi* groups in morphospace with *C. fatioi*.

Based on genetic, morphological and ecological data at least two species from the Lake Thun-Brienz radiation, namely *C. albellus* (since at least 2004: Bittner 2009; Vonlanthen and Périat 2018; this study) and *C. profundus* (since at least 2016: this study) have colonized Lake Biel. There are no indications and no historical records that the Bernese cantonal officials have translocated any whitefish from other lakes into Lake Biel. Importantly, Steinmann (1950) already mentions that fishermen reported that suddenly after the Jura water correction, whitefish that resembled *C. albellus* (common name Brienzlig), appeared in Lake Biel. It is hence possible, that colonization of Lake Biel happened in recent times through the river Aare, which became connected with

Lake Biel after the Jura water correction of 1868–1878. At least one of the species, *C. albellus*, has likely established a self-sustaining population in Lake Biel, since a reasonable number of ripe specimens of this species have been caught repeatedly over several years during the typical spawning period of this species (late summer: September–October; Bittner 2009; Vonlanthen and Périat 2018; Suppl. material 1: Figure S9). Today, Lake Biel harbours two native whitefish species, *C. confusus*, Fatio 1885 and *C. palaea*, Cuvier 1829 (Kottelat and Freyhof 2007) but it used to harbour a third species known by its local name as “Balch-Pfärrit” (Fatio 1885), which is extinct today (Vonlanthen et al. 2012). Fatio (1890: Page 192) mentions that the “Balch-Pfärrit” was intermediate in phenotype between *C. confusus* and *C. palaea* of Lake Biel and has been considered by the local fishermen as a natural hybrid between the latter two species. Yet, based on the overall phenotype and ecological characters (spawning season and depth) Fatio (1885, 1890) considered the “Balch-Pfärrit” as an independent albeit variable species. This species increased in abundance during the study period of Fatio, which coincided with the completion of the Jura water correction from 1868–1878 that by passed the river Aare from Lake Thun to Lake Biel. This led some fishermen to suggest, that the “Balch-Pfärrit” might have come from Lake Thun. Fatio dismissed this because these fish did not resemble the species known by then from Lake Thun, this being *C. albellus*, *C. alpinus* and *C. fatioi*. He rather suggested the rise in abundance of the “Balch-Pfärrit” may have been caused by the lake level reduction of Lake Biel following the Jura water correction. The Lake Biel and Lake Neuchatel species’ *C. confusus*, *C. palaea*, and *C. candidus* form distinct monophyletic clades in population neighbour-joining trees and one genetic cluster in a structure analysis, based on microsatellite and genomic AFLP loci (Hudson et al. 2011, 2016). Based on this and on the fact that the historically reported three whitefish species of Lake Biel (*C. confusus*, *C. palaea* and the “Balch-Pfärrit”) were all winter spawners (Fatio 1885, 1890; Steinmann 1950) and that the ripe whitefish, that were caught in recent years in late summer in Lake Biel, were assigned with high probability to whitefish species from Lake Thun (Bittner 2009; Suppl. material 1: Figure S9), suggests that the ripe specimens caught in late summer in Lake Biel are unlikely to be the extinct “Balch-Pfärrit”. Instead, we suggest that two Lake Thun whitefish species, *C. profundus* and *C. albellus*, have colonized Lake Biel. Interestingly, Steinmann (1950) reports that he was able to examine two ripe whitefish in September 1944 from Lake Biel that he thought resembled, based on their morphology (e.g., gill raker number, eye size), very much *C. albellus* from lakes Thun and Brienz.

Lakes Thun and Brienz in the Bernese Highlands today harbour the most speciose pre-alpine whitefish radiation. These lakes have also suffered the least anthropogenic pressures of all the large pre-alpine lakes in Switzerland. Species delineation and description in such rich radiations require an integrative approach to taxonomy, combining morphology with population genetics and ecology and extensive contemporary and historical specimen collections. Such work is also much needed for conservation-minded fisheries management because, as we have shown here and others before us (Douglas and Brunner 2002; Bittner 2009; Dönz et al. 2018), human-made changes to the connectivity of water bodies as well as deliberate introductions, are increasing the distribution ranges of species and cause previously isolated biota to mix.

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## Supplementary material I

### Tables S1–S8, Figures S1–S11

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Data type: measurements

Explanation note: **Table S1.** PC-loadings of all characters (values > 0.1 or < -0.1 are highlighted in bold), eigenvalues, proportion of explained variance, and R-squared from a linear regression of shape vs. isosize of the retained first three PC-axes from a PCA with all contemporary specimens of the formerly described species *C. alpinus*, *C. albellus*, and *C. fatioi* and their types and the newly described species *C. steinmanni* and *C. profundus* from Lake Thun. **Table S2.** PC-loadings of all characters (values > 0.1 or < -0.1 are highlighted in bold), eigenvalues, proportion of explained variance, and R-squared from a linear regression of shape vs. isosize of the retained first three PC-axes from a PCA with all contemporary specimens of the six species *C. alpinus*, *C. steinmanni*, *C. fatioi*, *C. albellus*, *C. acrinasus* and *C. profundus* from Lake Thun. **Table S3.** PC-loadings of all characters (values > 0.1 or < -0.1 are highlighted in bold), eigenvalues, proportion of explained variance, and R-squared from a linear regression of shape vs. isosize of the retained first three PC-axes from a PCA with all contemporary specimens of the four species *C. alpinus*, *C. fatioi*, and *C. albellus* and the newly described species *C. brienzi* from Lake Brienz. Only specimens smaller than 163.5 mm were used for the analysis to overcome allometry issues. **Table S4.** PC-loadings of all characters (values > 0.1 or < -0.1 are highlighted in bold), eigenvalues, proportion of explained variance, and R-squared from a linear regression of shape vs. isosize of the retained first three PC-axes from a PCA with all specimens of the three species *C. alpinus*, *C. fatioi*, and *C. albellus* and the newly described species *C. brienzi* from Lake Brienz. **Table S5.** PC-loadings of all characters (values > 0.1 or < -0.1 are highlighted in bold), eigenvalues, proportion of explained variance, and R-squared from a linear regression of shape vs. isosize of the retained first three PC-axes from a PCA with all whitefish species from Lake Thun and the three specimens of whitefish from Lake Biel that were assigned by genotype to *C. albellus* or *C. profundus*. **Table S6.** Frequency of occurrence of meristic values in the six whitefish species from Lake Thun and the four whitefish species from Lake Brienz. **Table S7.** Frequency of occurrence of the meristic values in the four whitefish species from Lake Constance, Switzerland, *C. gutturosus* Gmelin, 1818, *C. arenicolus* Kottelat, 1997, *C. macrophthalmus* Nüsslin, 1882, *C. wartmanni* Bloch, 1784, and the partially allochthonous whitefish species *C. acrinasus* from Lake Thun, Switzerland, that has ancestry contributions from Lake Constance whitefish. **Table S8.** PC-loadings of all characters (values > 0.1 or < -0.1 are highlighted in bold), eigenvalues, proportion of explained variance, and R-squared from a linear regression of shape vs. isosize of the retained first three PC-axes from a PCA with all contemporary specimens of the formerly described species *C. alpinus*, *C. albellus*, and

*C. fatioi*, their types, the newly described species *C. steinmanni* and *C. profundus* from Lake Thun and the museum specimens with the river Aare as type-locality. **Figure S1.** Illustration of the morphological body character measurements (see Table 1 in materials and methods for a detailed description of each character). **Figure S2.** Illustration of the morphological head character measurements (see Table 1 in materials and methods for a detailed description of each character). **Figure S3.** Spawning distribution of the different whitefish species at one spawning site in Lake Thun (Faulensee: 46.673725 / 7.707944) and Lake Brienz (Iseltwald: 46.712079 / 7.961261) during the complete spawning season of the whitefish species from late summer to late winter. **Figure S4.** Size (TL=total length in mm) at age of the species *C. alpinus* (A), *C. albellus* (B) *C. steinmanni* (C), *C. fatioi* (D), *C. acrinasus* (E), and *C. profundus* (F) from Lake Thun. **Figure S5.** Size (TL = total length in mm) at age of the species *C. alpinus* (A), *C. albellus* (B), *C. brienzii* (C), and *C. fatioi* (D) from Lake Brienz. **Figure S6.** Size (TL = total length in mm) of 3-year-old fish of the species *C. acrinasus* (red), *C. alpinus* (blue), *C. steinmanni* (light blue), *C. albellus* (green), *C. profundus* (orange), *C. fatioi* (violet) and *C. brienzii* (black) from lakes Thun (A) and Brienz (B). **Figure S7.** The “cheetah look” of some specimens of *C. albellus* from Lake Brienz with rather large pigmented dots arranged more or less in rows on the upper dorsum. **Figure S8.** The three main colouration types found on the dorsum and the dorsal part of the flanks above the lateral line in the whitefish species of Lakes Thun and Brienz. **Figure S9.** Scatterplot of the first three shape PC axes and the total number of gill rakers for the contemporary whitefish species from Lake Thun and the three contemporary specimens of whitefish from Lake Biel that were caught on the 9th of October 2016 and were genetically assigned (see Materials and methods for details on the genetic assignments) to *C. albellus* (specimens NMBE-1077160 with 84% and NMBE-1077159 with 94% genetic assignment) or *C. profundus* (specimen NMBE-1077158 with 96% genetic assignment). **Figure S10.** Map of Lake Thun, Brienz, and Biel and the locations where all contemporary specimens of the six species of Lake Thun (*C. alpinus*, *C. steinmanni*, *C. fatioi*, *C. albellus*, *C. acrinasus*, and *C. profundus*) and the four species of Lake Brienz (*C. alpinus*, *C. brienzii*, *C. fatioi*, *C. albellus*) were caught as well as the locations of the contemporary specimens of the 2 whitefish species from Lakes Thun and Brienz that were caught in Lake Biel. **Figure S11.** Principal Component Analysis showing that the whitefish specimens caught in the river Aare at the end of the 19th century and mid-twentieth century (locality: either near the city of Bern (specimens: NMBE-1013589 and NMBE-1013603), below the outflow of Lake Thun near the city of Thun (specimens: Eawag-363-1 and Eawag-363-2) or in the Bödeli-Aare between the lakes Thun and Brienz near the city of Interlaken (specimens: Eawag-373-1 and Eawag-373-2) lie within the range or adjacent to the range of the contemporary specimens of *C. fatioi*.

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