RESEARCH ARTICLE



A remarkable new cave scorpion of the family Pseudochactidae Gromov (Chelicerata, Scorpiones) from Vietnam

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Abstract

A new genus and species of scorpion belonging to the family Pseudochactidae are described based on four specimens collected in the Tien Son cave at the Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam. The new species represents a true troglobitic element, the first one known for the family Pseudochactidae. This represents the third known record of a pseudochactid, and the first from Vietnam.

Keywords

Scorpion, Vietnam, Phong Nha - Ke Bang National Park, karst cave system, new genus and species, troglobitic element

Introduction

One of the most remarkable scorpions described during the last 30 years is *Pseudochactas ovchinnikovi* Gromov, 1998, discovered in an isolated mountainous region of southeastern Uzbekistan and southwestern Tajikistan in Central Asia. Although this

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scorpion shares some features with buthid and nonbuthid scorpions, it is remarkable because it displays a number of characters unique among recent (extant) scorpions, including a distinct trichobothrial pattern. This led Gromov (1998) to create a new monotypic family, the Pseudochactidae Gromov, 1998.

Subsequently, authors have not reached a consensus regarding the phylogenetic position of this enigmatic scorpion. Based on its peculiar trichobothrial pattern, Fet (2000) suggested a relationship to the most plesiomorphic Buthidae C. L. Koch, 1837 or to Chaerilidae Pocock, 1893. Lourenço (2000) placed *Pseudochactas* in a new superfamily, Chaeriloidea Pocock, 1893, implying that he considered it to be the sister group of *Chaerilus*. Although there is widespread agreement that *Pseudochactas* is basal within recent scorpions, its precise phylogenetic position remains a matter of debate (Fet et al. 2004). In an exhaustive study of *P. ovchinnikovi*, Prendini et al. (2006) concluded that the most plausible position for this 'living fossil' would be as the sister-group of Buthidae.

Shortly after these publications, a second genus and species belonging to the family Pseudochactidae, *Troglokhammouanus steineri* Lourenço, 2007, was described from karst caves in Laos (Lourenço 2007a). This new element of the Pseudochactidae reopened the question about the origins and affinities of this family and led to new biogeographical interpretations (Lourenço 2007a). The precise morphology of this new pseudochactid scorpion was also complemented by SEM studies and a further comparison with elements of the family Chaerilidae (Lourenço 2007b).

Since the description of *T. steineri* (Lourenço 2007a, b), no new insights have been published on this subject. While prospecting scorpions in a karst cave system in Vietnam, the second author was able to collect several specimens of a new pseudochactid scorpion. These are described here as a new genus and species. In this note we do not propose new phylogenetic or biogeographical considerations, since these have already been largely discussed by Lourenço (2007a). It is important, however, to notice that the new Vietnamese pseudochactid comes from caves belonging to the same karst system as those in which *T. steineri* was found in Laos. This could suggest that this region of Southeast Asia may represent a refuge or an endemic centre for elements of this family. Finally, as suggested by Prendini et al. (2006), the discovery of *P. ovchinnikovi* could represent the most remarkable scorpion discovery during the last (20th) century. In this same vein, the discoveries of two new genera and species of pseudochactids in Laos and Vietnam are far from negligible.

Orogeny and geodynamics of South East Asia

The Southeast Asia or Indochina tectonic plate forms the core of the geological structure of southeastern Asia. This plate comprises the countries of Vietnam, Laos, Cambodia and western Thailand, but according to Metcalfe (2002), also the southeastern portion of the Malayan Peninsula, a fragment of Sumatra, and westernmost portion of Borneo.



Figure 1. Tien Son Cave, internal view, showing second author searching for scorpions.

The Southeast Asia plate originated during the Proterozoic. It became detached during Palaeozoic and drifted northward. The carbonate platforms were developed during the Devonian-Late Palaeozoic. The Palaeozoic history of detachment and collision is quite speculative. The equivalent of Caledonian orogeny, followed by the formation of the Palaeotethys Ocean is quite possible. Climate records indicate major differences between Sibumasu, Indochina and South China during the Late Palaeozoic. During the Triassic, as a result of the Indosinian orogeny and closure of the Palaeotethys Ocean, the Southeast Asian plate joined the Asian continent (Metcalfe 2002; Senghor and Hsü 1985; Golonka et al. 2006).

Geology and ecology of the region

In Central Vietnam, the dominant geological feature is the Truong Son Range. This string of mountains and plateaus, also known as the Annamite Mountain Range, is roughly 1200 km long and 50–75 km wide, intersected by passes and lowlands. Most of its hills lie between elevations of 500–2000 m, and for much of its distance they run parallel to the central coastline, straddling the border with Laos. Central Vietnam's



Figure 2. Site in the cave where scorpions were found.

Truong Son Range is a transitional region between the subtropical communities of the North and the tropical ones of the South, and it harbours many endemic species (Groves and Schaller 2000; Herrmann et al. 2002). The Truong Son Range can be divided into three regions: (i) the Northern Truong Son, with much of its region being composed of ancient marine basins, that have been uplifted and now are heavily eroded and form the characteristic sharp karst ridges and peaks with extensive systems of caves, tunnels, and underground rivers and streams; (ii) the Central Truong Son, dominated by the Kon Tum Massif: an enormous, largely granitic formation, which is among the oldest exposed rocks in Southeast Asia; and (iii) the Southern Truong Son, including Vietnam's remaining uplands with Dac Lac, Da Lat and Di Linh Plateaus, a series of eroded granite and basalt plateaus dotted with isolated peaks. In the Northern Truong Son, Phong Nha - Ke Bang is a region located within the most extensive tracts of limestone karst habitat in Asia. This unique karst system (290–255 My) was likely uplifted in the early Triassic, differs substantially in terms of both geology and habitat from adjacent regions (Sterling et al. 2006; Ziegler 2008; Ziegler and Vu 2009).

The Phong Nha-Ke Bang karst is the oldest major karst area in Asia. It has been subject to massive tectonic changes and comprises a series of rock types that are interbedded in complex ways. Probably as many as seven different major levels of karst development have occurred as a result of tectonic uplift and changing sea levels, thus the karst landscape of PNKB is extremely complex with high geodiversity and many geomorphic features of considerable significance. There is also strong evidence that sulphuric dissolution and hydrothermal action have played an important role in shaping the general landscape and the caves, though this has not yet been properly assessed.

Modern Phong Nha-Ke Bang is a result of five stages in the Earth's crustal development and movement: Late Ordovician - Early Silurian Stage (about 450 My), Middle-late Devonian Stage (about 340 My), Carboniferous-Permian (about 300 My), Mesozoic Orogenic stage, and Cenozoic stage (Ziegler and Vu 2009; UNEP-WCMC 2006).

Location, ecology and climate of the national park and caves

Phong Nha - Ke Bang (Vietnamese: *Vuròn quốc gia Phong Nha-Ké Bàng*) is now a national park and UNESCO World Heritage Site in the Bố Trạch and Minh Hóa Districts of central Quang Binh Province, in north-central Vietnam, about 500 km south of Hanoi. The park borders the Hin Namno Nature Reserve in the province of Khammouan, Laos (Mouret 2001) in the west, 42 km east of the South China Sea. Phong Nha-Ke Bang National Park is situated in a limestone zone of 2000 km² in Vietnamese territory and borders another limestone zone of 2000 km² of Hin Namno in Laotian territory. The core zone of this national park covers 857.54 km² and a buffer zone covers 1954 km². The park was created to protect one of the world's two largest karst regions, with 300 caves, and also protects the ecosystem of limestone forest of the Annamite Range region along the north-central coast of Vietnam.

Phong Nha-Ke Bang area is noted for its cave systems with a total length of about 126 km; only 20 caves have been surveyed by Vietnamese and British scientists; 17 of these are located in the Phong Nha area and three in the Ke Bang area. Before discovery of Son Doong Cave, Phong Nha held several world cave records, as it has the longest underground river, as well as the largest caverns and passageways. The park derived its name from Phong Nha cave, the most beautiful of all.

Like northern Central Vietnamin general and Quang Binh Province in particular, the climate in this national park is tropical, hot, and humid. The annual mean temperature ranges from 23 to 25 °C, with extremes of 41°C in the summer and a 6°C in the winter. The hottest months in this region are from June to August, with an average temperature of 28°C, and the coldest months from December to February with an average temperature of 18°C. Annual rainfall is 2000–2500 mm, and 88% of the rainfall occurs from July to December. With more than 160 rainy days per year, no month is without rain. Mean annual relative humidity is 84% in forests.

Tien Son Cave, where the new scorpion was found is located in Son Trach Commune, Bố Trạch District. The entrance is located 1 km from Phong Nha Cave, at an altitude of 200 m. Tien Son Cave is 980 m in length. A 10 m deep hole is situated 400 m from the entrance, after which a 500 m long underground cave is open exclusively to professional scientists. Like Phong Nha Cave, this cave features spectacular stalactites and stalagmites. According to British speleologists, Tien Son Cave was created tens of millions years ago, when a water current holed this limestone mountain in Ke Bang. Following a series of movements of rocks, this mass was levered or lowered, blocking the current and creating what is now Tien Son Cave, while the flow of the underground river was redirected to Phong Nha Cave. Although Phong Nha and Tien Son Caves are located next to each other, there are no passages linking them (UNEP-WCMC 2006).

Methods

Scorpions were collected by the second author, while exploring the caves with the help of standard electric torches. Scorpions were found under some heavy flat rocks, about 200 m from the main cave entrance. Measurements and illustrations were made using a Wild M5 stereo-microscope with a drawing tube and an ocular micrometer. Measurements follow those of Stahnke (1970) and are given in mm. Trichobothrial notations are those developed by Soleglad and Fet (2001) and the morphological terminology mostly follows that of Hjelle (1990), Prendini et al (2006) and Lourenço (2007a,b).

Taxonomic Treatment

Family Pseudochactidae Gromov, 1998

Genus Vietbocap gen. n.

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Diagnosis. Cheliceral movable finger with three denticles (medial, subdistal, external distal) on dorsal edge; external distal denticle smaller than internal distal denticle. Anterior margin of carapace depressed with a moderate concavity, posterior margin shallowly recurved. Lateral ocelli absent. Pair of circumocular sutures with a broad U-shaped configuration (diagnostic for family), only vestigial and incomplete in the posterior region to median ocular tubercle. Median ocelli absent; median tubercle represented by a smooth depressed zone. Anterosubmedial carinae absent from zone limited by circumocular sutures. Type D trichobothrial pattern (Soleglad and Fet 2001, 2003a) with 35 trichobothria per pedipalp: 12 on femur, of which five dorsal, four internal and three external (d_1 , d_4 , d_5 and i_4 extremely reduced; i_4 absent, in one specimen); 10 on the patella, of which three dorsal, one internal, six external (*est* extremely reduced; absent in one specimen); ventral surface without trichobothria; 13 on the chela, of which five on manus, eight on fixed finger (*est* displaced to cutting edge of fixed finger); pedipalp femur dorsal trichobothria with 'beta-like' configuration. Sternum pentagonal, type 1 (Soleglad and Fet 2003b), moderately compressed hori-

zontally, markedly longer than wide, external aspect not flat, with a concave region, posteromedian depression round. Telotarsi each with several spinular setae not clearly arranged in rows. Metasomal segment V with a weakly marked pair of ventrosubmedian carinae; no ventromedian carina between ventrosubmedian carinae. Fixed and movable fingers strongly curved; dentate margins each with median denticle row comprising eight oblique granular subrows; internal and external accessory granules at base of each subrow. Respiratory spiracles small, semi-oval. Pro-and retrolateral pedal spurs present on legs I-IV. Tibial spurs absent from all legs.

Derivatio nominis: The generic name is a combination of *Viet* (for Vietnamese) and *bocap* (scorpion in Vietnamese language).

Type species: Vietbocap canhi sp. n.

Vietbocap canhi sp. n.

urn:lsid:zoobank.org:act:DBD6B87B-36F9-4F09-8584-B31ACB125634 Figs 3–24

Diagnosis: as for the genus.

Type material: male holotype; female and two male paratypes. Vietnam, Quang Binh Province, north-central Vietnam, Bố Trạch - Minh Hóa District, Phong Nha - Ke Bang National Park, Tien Son Cave ($106^{\circ}16'E - 17^{\circ}32'N$), mid section of cave (200 m from cave entrance), 16/V/2010 (D.-S. Pham). Holotype and female paratype are deposited in the collection of the Muséum national d'Histoire naturelle, Paris. The other paratypes are deposited in the collections of the Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi.

Patronym. In honour of Dr. Le Xuan Canh, Director of the Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, for his support of scorpion research in Vietnam.

Description: based on the male holotype and paratypes (measurements given in mm after the description).

Colour. General coloration yellowish to pale yellow; cheliceral teeth, telson tip and rows of granules on pedipalp fingers reddish-yellow to dark reddish.

Morphology. Chelicerae: dorsal edge of fixed finger, with four denticles (basal, medial, subdistal, distal); ventral edge with 4–5 very reduced denticles; movable finger with three denticles (medial, subdistal, external distal) on dorsal edge, without basal denticles; ventral edge with 4–5 reduced denticles; external distal denticle smaller than internal distal denticle; ventral aspect of fingers and manus with numerous macrose-tae. Carapace. Anterior margin depressed with a moderately marked concavity. Lateral ocelli absent. Median ocular tubercle represented by a smooth depressed zone; median ocelli absent; interocular furrow obsolete. One pair of vestigial circumocular sutures with a broad U-shaped configuration, incomplete behind median ocular tubercle. Anteromedian and posteromedian furrows shallow; posterolateral furrow shallow, weakly curved; posteromarginal furrow narrow, very shallow. Carapace almost totally smooth,



Figsure 3–6. *Vietbocap canhi* sp. n., male holotype and female paratype, dorsal and ventral aspects. Scale bar = 10 mm.

except for some isolated granules anteriorly; acarinate; anterosubmedial carinae absent from the zone internal to circumocular sutures. Pedipalp segments apilose. Femur with five discernible carinae, all weak to vestigial; intercarinal surfaces smooth. Patella with 5–6 discernible carinae; ventrointernal carinae with some spinoid granules; intercarinal surfaces smooth. Chela with only vestigial carinae, rounded and smooth. Fixed and movable fingers strongly curved; dentate margins each with median denticle row comprising eight oblique granular sub-rows; each sub-row comprising several small granules and internal and external accessory granules. Trichobothria: Orthobothriotaxic, Type D (Soleglad and Fet 2001, 2003a), 'beta-like' configuration, d_2 situated on



Figsure 7–11. *Vietbocap canhi* sp. n. (M=male, F=female). **7** Carapace, dorsal aspect (M) **8** Chelicera, dorsal aspect (F) **9–10** Ventral aspect, showing sternum, genital operculum, pectines and sternite III (M & F) **11** Leg IV, showing absence of tibial spur and telotarsi with spinular setae (F). Scale bars = 1 mm.



Figsure 12–15. *Vietbocap canhi* sp. n. (M=male, F=female). **12–13** Metasomal segment V and telson, lateral and ventral aspects (M) **14** Idem female **15** Movable finger of pedipalp chela with subrows of granules (M). Scale bars = 1 mm.



Figures 16–18. *Vietbocap canhi* sp. n., female paratype. Trichobothrial pattern. Chela, dorso-external, ventral and internal aspects. Scale bar = 1 mm.

dorsal surface, d_3 and d_4 in same axis of the femur, parallel and closer to dorsoexternal carina than is d_1 , angle formed by d_1 , d_3 and d_4 opening toward internal surface; totals: femur, 12 (five dorsal, four internal, three external); patella, 10 (three dorsal, one internal, six external); chela, 13 (five manus, eight fixed finger). Legs I to IV: tibiae, without spurs; basitarsi each with a pair of pro- and retrolateral spurs; telotarsi each with several spinular setae, not well arranged in rows. Sternum pentagonal, type 1 (Soleglad and Fet 2003b), moderately compressed horizontally, markedly longer than wide, external aspect not flat, with a concave region, posteromedian depression round. Pectines each with 3–4 distinct marginal lamellae in male and female, 8–9 well-delineated median lamellae present in male (7 in female). Fulcra absent or vestigial. Pectinal tooth count: 9–9 in males and 7–7 in female. Genital operculum completely divided longitudinally;



Figures 19–24. *Vietbocap canhi* sp. n., female paratype. Trichobothrial pattern. **19–21** Femur, internal, dorsal and external aspects **22–24** Patella, dorsal, external and ventral aspects. Scale bar = 1 mm.

genital plugs observed in male. Mesosoma: pre-tergites smooth and shiny; post-tergites II-VI smooth, apart from some minute granules; VII with a few granules and a pair of dorsosubmedian and dorsolateral carinae, reaching posterior edge of segment. Sternites almost entirely smooth, acarinate; surfaces with scattered macrosetae; distal margins with sparse row of macrosetae; respiratory spiracles small, semi-oval in shape. Meta-soma covered in short macrosetae. Ten carinae on segments I to III; eight carinae on segment IV; four on segment V. Dorsosubmedian carinae moderately developed on segments I-IV, absent on segment V; spinoid granules absent. Other carinae moderately to weakly developed on segments I-V. Telson long and slender; vesicle smooth on all faces; aculeus shorter than vesicle and weakly curved, without a subaculear tubercle ventrally. Form of venom glands unknown.

Geographic distribution. Only known from the type locality.

Measurements (in mm) of male holotype/female paratype. Total length 22.4/21.3. Carapace: length 2.9/2.8; anterior width 2.0/1.8; posterior width 3.2/2.9. Mesosoma length 5.5/6.4. Metasomal segments: I, length 1.2/1.0, width 1.4/1.2; II, length 1.4/1.2, width 1.3/1.0; III, length 1.5/1.4, width 1.2/0.9; IV, length 2.1/1.7, width 1.1/0.8; V, length 3.9/3.2, width 1.1/0.8, depth 0.9/0.8. Telson length 3.9/3.6; vesicle length 2.4/2.2, width 1.3/1.0, depth 1.2/0.9. Pedipalp: femur length 3.8/3.1, width 0.9/0.7; patella length 3.6/3.2, width 1.1/0.9; chela length 7.1/5.8, width 1.2/1.0, depth 1.0/0.9; movable finger length 4.2/3.9.

Key to the known genera and species of Pseudochactidae

1	Median and lateral ocelli present; leg tibial spurs present
2	Median and lateral ocelli absent; leg tibial spurs absent Vietbocap canhi sp. n.
3	Circumocular sutures incomplete; peg sensillae of pectines rounded
	Troglokhammouanus steineri Lourenço, 2007
_	Circumocular sutures complete; peg sensillae of pectines spatular
	Pseudochactas ovchinnikovi Gromov, 1998

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RESEARCH ARTICLE



Revision of the key characters for the *Thricops nigrifrons* species-group (Diptera, Muscidae)

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Abstract

An analysis of key characters for the separation of *Thricops nigrifrons* and *T. longipes* (Diptera, Muscidae) is given. A revised key for *T. nigrifrons* and related species, including two species recently described from the Caucasus, is proposed.

Keywords

Thricops nigrifrons, Thricops longipes, Muscidae, key

Introduction

The *Thricops nigrifrons* species-group is characterized by: long-plumose arista; dark body; holoptic head in male; absence of apical spur on *t3* and of apical spurs on *t1* in males; *t2* without *pv* or *v* seta(e); lower margin of face not projecting; 4 postsutural *dc*; unmodified fore tarsomeres in male; mid tarsomeres 3–4 each with a row of pale *pv* setulae in male (except *T. dawkinsi*); the male terminalia are similar (*T. semicinereus* - type).

Thricops nigrifrons (Robineau-Desvoidy, 1830) and *T. longipes* (Zetterstedt, 1845) are widespread in the Palearctic region. Nevertheless Hennig (1962), d'Assis-Fonseca (1968), Gregor et al. (2002) and Savage (2003) have given different and often contradictory recommendations on how to separate these species. Recently two new related species have been described from the Russian Caucasus, *T. tomkovichi* Vikhrev, 2009 and *T. dawkinsi* Vikhrev, 2009 (Vikhrev and Sorokina 2009), and this has necessitated a revision of the characters for the separation of *T. nigrifrons* and *T. longipes*.

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The examined material is restricted to Eastern Europe, Transcaucasian region and Siberia, and do not include specimens collected in Western Europe. However, the proposed key characters are expected to be suitable for west-european specimens as well, because there is no gap in natural habitats of *nigrifrons* and *longipes* in Europe. Another reason is the fact that d'Assis-Fonseca (1968) came to the same main conclusions based on the investigation of the material from British Islands.

Material and methods

This analysis is based on the following material:

- **Thricops dawkinsi** Vikhrev, 2009 23 ♂♂ and ♀♀. **Russia:** Karachay-Cherkessia, Krasnodar, North Ossetia. Holotype in Zoological Museum of Moscow University, Moscow, (ZMMU), paratypes in ZMMU, Zoological Institute, St. Petersburg (ZIN), and the Natural History Museum, London (BMNH).
- Thricops longipes (Zetterstedt, 1845) 140 ♂♂ and ♀♀. Estonia. Russia (European): Arkhangelsk, Chelyabinsk, Karachay-Cherkessia, Karelia, Komi, Krasnodar, Moscow, Murmansk, Novgorod, St-Petersburg, Ulyanovsk. Russia (Asian): Altai Rep (=Gorno-Altai), Khanty-Mansi, Krasnoyarsk, Novosibirsk, Tomsk, Yamalo-Nenets (ZMMU and ZIN).
- **Thricops nigrifrons** (Robineau-Desvoidy 1830) 150 ♂♂ and ♀♀. **Estonia. Turkey:** Bolu prov. **Russia (European):** Chelyabinsk, Moscow, St Petersburg, Vladimir, Yaroslavl. **Russia (Asian):** Krasnoyarsk, Novosibirsk, Tomsk (ZMMU and ZIN).
- *Thricops tomkovichi* Vikhrev, 2009 62 ♂♂ and ♀♀. **Russia:** Karachay-Cherkessia, Krasnodar. Holotype in (ZMMU), paratypes in ZMMU, ZIN and BMNH.

Morphological structures are abbreviated as: f1, t1, f2, t2, f3, t3 = fore, mid, hind, femur or tibia; ac = acrostichal setae; dc = dorsocentral setae; a, p, d, v = anterior, posterior, dorsal, ventral seta(e).

Notes on the identification of T. nigrifrons and T. longipes

On several occasions colleagues have expressed doubts that *T. nigrifrons* could be reliably separated from *T. longipes*. I have shared these doubts too, but currently I am convinced that a reliable (and rather easy) separation is possible. Let us first consider the identification characters proposed by Hennig (1962), d'Assis-Fonseca (1968), Gregor et al. (2002) and Savage (2003).

The longest aristal hairs distinctly longer than width of postpedicel *nigrifrons* The longest aristal hairs slightly longer than width of postpedicel.... *longipes* This character was used as the main one by all the cited authors except for
 Gregor et al. (2002), although the estimation of length and wording differ.

I agree that the aristal hairs are somewhat longer in *nigrifrons*, but I disagree with using this as the main character: the difference is very fine and the character is variable, with overlapping taking place. Gregor et al. (2002) gave the following measurements: *nigrifrons* – longest aristal hairs 1.05–1.30 times as long as width of postpedicel; *longipes* – 0,85–1.15 times. Instead of the length of aristal hairs Gregor et al. (2002) proposed the following wording:

- Female: long aristal hairs reaching apical third of arista *nigrifrons* Female: long aristal hairs not reaching apical third of arista *longipes* I have not found this alternative to be more reliable or easier in use than the previous one.
- 3 Male with p and v setulose hairs on basal half of f hardly longer than depth of femur......nigrifrons Male with p and v setulose hairs on basal half of f3 quite twice as long as depth of femur......longipes Used by d'Assis-Fonseca (1968), but the other authors excluded this character from their keys. According to the descriptions given by Savage (2003): in longipes " $f3 \dots p$ and v surfaces covered with long hairs, longer than depth of femur"; in *nigrifrons "f3 ... p* and *v* surfaces covered with setae of variable length, as long to much longer than depth of femur". I suppose that the source of the misunderstanding is that the fine hairs on the p and v surface of f3 are not homogeneous. In *longipes*, these hairs really are evenly long, at least twice as long as femoral width, but in *nigrifrons* the hairs on the *p* surface are rather long, usually about 1-1.5 times as long as femoral width, but on the v surface they are short, especially in basal half of femur where the hairs are 0.5–1 times as long as femoral width. Thus, the fine hairs on f3 are distinctly longer in *longipes* than in *nigrifrons*, but the difference is the most obvious in a comparison of the v hairs in the basal half of f3, for which the hind femur needs only to be observed in lateral view. Among about 150 male specimens examined by me, this character was always reliable and correlated with other characters. No specimens with an intermediate development of f3 setulae were found.

4	Male $t3$ with pv present in apical $1/2$	nigrifrons
-	Male $t3$ with pv present in apical $2/3$	longipes

Proposed by Hennig (1962), but excluded by later authors. I agree with the exclusion of this variable character.

- Male notopleuron bare......nigrifrons
 Male notopleuron with a few setulae......longipes
 Proposed by Savage (2003). In fact the notopleuron is setulose on the anterior part in both species. The notopleuron on the surface between the anterior and posterior setae is almost always bare in *nigrifrons* and usually setulose in *longipes*, but bare in a quarter of the examined specimens. This may be used as an additional character only.
- Male abdomen with the median vitta on tergite 3 inconspicuous... *nigrifrons* Male abdomen with a conspicuous black median vitta on tergite 3 ... *longipes* Proposed by Vikhrev and Sorokina (2009). The trace of a narrow and less dusted median vitta may be present in *nigrifrons*, but otherwise this character separates all examined specimens.
- 9 Female: postsutural part of scutum in posterior view with the median vitta indistinct, or if more or less distinct then narrow, widened only posteriorly.
 nigrifrons Female: postsutural part of scutum in posterior view with the undusted median vitta distinct, uniformly wide throughout, occupying all the area between acrostichal rows.



Figure 1. Female scutum in posterior view. **a** *nigrifrons* without median vitta **b** *nigrifrons* with narrow median vitta **c** *longipes*.

Proposed by d'Assis-Fonseca (1968), but with a misprint, so the indistinct vitta was wrongly ascribed to *longipes* and the distinct one to *nigrifrons*. Probably because of this, no one else has drawn attention to this reliable character, which separates all the females I have examined (Fig. 1).

10	Female abdomen with the median stripe narrow, often absent nigrifrons
_	Female abdomen with a broad median stripe longipes
	Again proposed by d'Assis-Fonseca (1968), and again with the characters
	for <i>longipes</i> and <i>nigrifrons</i> transposed. Usually present in <i>longipes</i> , present or absent in <i>nigrifrons</i> . I think it is better to exclude this character.
	8 5

11	Female: <i>t3</i> with only 2 <i>ad</i> setae	nigrifrons
_	Female: <i>t3</i> with 3–4 <i>ad</i> setae	longipes
	Used by Hennig (1962) and Savage (2003). Correct in	n the vast majority of
	specimens.	

12	Female: dusting on thorax and abdomen yellow with a slight brown tint
	nigrifrons
_	Female: dusting on thorax and abdomen grey with a slight yellow tint
	longipes
	Proposed by Savage (2003). I agree that usually <i>nigrifrons</i> has more yellowish
	dusting while <i>longipes</i> is more greyish, but the reverse situation may also oc-
	cur. Personally I find this character difficult to use and prefer not to include
	it in the key.

Distribution. The distribution of these species in mountain areas seems sporadic and there aren't enough reliable records. In the Austrian Alps, in the Oetz Valley, both species overlap at about 1500 m asl. Below this level, in the coniferous and broad-leaf for-

est zone, *nigrifrons* is found; above it, in the upper forest zone and above the tree-line, only *longipes* is found (A.C. Pont, pers. comm.). In the Russian Caucasus (Krasnodarsky Kray and Karachay-Cherkessia) *longipes* is found at the altitudes 1800–2500 m asl., while *nigrifrons* is not found. In the mountain area in Turkey, Bolu prov., 40.6N 31.8E *nigrifrons* is found at the altitudes 1450–1950 m asl., while *longipes* is not found. In European Russia *nigrifrons* is common in the area between Moscow and St. Petersburg (55–60°N), but absent or at least rare in Karelia at 65°N. The southern border of distribution of *longipes* seems to be the northern part of Moscow region (56°N), it is common in the northern coniferous forest zone (taiga) and is still the dominant species in the tundra around Vorkuta (67.5°N). In Abisko National Park (North Sweden, 68°N), with birch forest and mountain tundra (A.C. Pont, pers. comm.) and in birch-willow forest in Murmansk (69°N) only *longipes* was found.

Key for the Thricops nigrifrons species-group

Males

1	f2 with a comb of 3–4 long and strong setae on <i>p-pv</i> surface at base and the fine setae in <i>av</i> and <i>pv</i> rows 1.5–2 times as long as $f2$ width. Legs at least partly yellowish (tibiae) or both tibiae and femora yellow. $t3$ with a comb of ventral preapicals consisting of 3–4 long curved setae. Caucasus
_	f2 without such a comb of setae on <i>p-pv</i> surface at base and the setae in <i>pv</i> and <i>av</i> rows short, at most as long as femoral width. Legs entirely black. $t3$ with 1–2 shorter ventral preapical setae. Palearctic, including Transcaucasian region
2	Femora black, tibiae more or less darkened basally. Mid tarsomeres 3-4 each
	with a row of pale pv setulae. Fore tarsus on p -surface with fine hairs that are
	1.5 times as long as tarsal width tomkovichi Vikhrev
_	All femora and tibiae yellow, at most fore femur slightly darkened. Mid tar-
	someres $3-4$ each with the row of pale pv setulae reduced. Fore tarsus with the
	<i>p</i> -hairs not longer than tarsal width <i>dawkinsi</i> Vikhrev
3	<i>p</i> -hairs not longer than tarsal width <i>dawkinsi</i> Vikhrev In lateral view, <i>f3</i> on basal half with fine hairs on <i>v</i> surface at most as long as
3	<i>p</i> -hairs not longer than tarsal width <i>dawkinsi</i> Vikhrev In lateral view, $f3$ on basal half with fine hairs on v surface at most as long as femoral width, much shorter than the strong <i>av</i> setae (the hairs on <i>p</i> surface
3	<i>p</i> -hairs not longer than tarsal width
3	<i>p</i> -hairs not longer than tarsal width
3	<i>p</i> -hairs not longer than tarsal width
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surface at least twice as long as femoral width). In posterior view, postsutural part of scutum subshining black with only thin greyish dusting, consisting of two vittae restricted to areas between *ac* rows and slightly beyond *dc* rows, median vitta between *ac* rows always present. Abdomen with a black subshining median vitta on tergite 3 wide and distinct on at least anterior 2/3 of tergite. Frons with all setulae on upper half reclinate. Secondary characters: body length usually 8.5–9 mm, rarely 7.5–9.5 mm, ground setulae usually (in 75% specimens) present between the two notopleural bristles, longest aristal hairs 0.85–1.15 times as long as width of postpedicel*longipes* (Zetterstedt)

Females

1	Legs entirely black. Palearctic, including Transcaucasian region2
_	Legs partly or entirely yellow. Caucasus
2	Postsutural part of scutum in posterior view with the median vitta indistinct
	(Fig. 1a), or if more or less distinct then narrow, sometimes slightly widened
	posteriorly (Fig. 1b). t3 with only 2 ad setae. Longest aristal hairs 1.05-1.30
	times as long as width of postpedicel. Body length usually 6.5–7.5 mm
	nigrifrons (Robineau-Desvoidy)
_	Postsutural part of scutum in posterior view with the undusted median vitta
	distinct, uniformly wide throughout, occupying all the area between ac rows
	(Fig. 1c). t3 with 3-4 ad setae, the additional seta(e) often short. Longest
	aristal hairs 0.85-1.15 times as long as width of postpedicel. Body length
	usually 7.5–9 mmlongipes (Zetterstedt)
3	Femora black, tibiae darkened basally tomkovichi Vikhrev
_	Femora and tibiae yellow
	-

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RESEARCH ARTICLE



Systematics of the Neotropical caddisfly genus Notidobiella Schmid (Trichoptera, Sericostomatidae), with the description of 3 new species

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Abstract

Three new species of *Notidobiella* Schmid (Insecta: Trichoptera) are described from South America: *Notidobiella amazoniana* **sp. n.** (Brazil), *N. brasiliana* **sp. n.** (Brazil), and *N. ecuadorensis* **sp. n.** (Ecuador). In addition, the 3 previously described species in the genus, *N. chacayana* Schmid, *N. inermis* Flint, and *N. parallelipipeda* Schmid, all endemic to southern Chile, are redescribed and illustrated, including the females of each species for the first time, and a key to males of the species in the genus is provided. The occurrence of *Notidobiella* in Brazil and Ecuador represents a significant extension of the range of the genus beyond southern Chile where it previously was thought to be endemic. The biogeography of Sericostomatidae and other austral South American Trichoptera is reviewed. The presence of the family in South America may not be part of a "transantarctic" exchange, but instead may represent an earlier occurrence in the region. The distribution of *Notidobiella* in tropical South America likely represents recent dispersal from southern South America to the north.

Keywords

caddisfly, Neotropics, transantarctic, new species, biogeography, South America, taxonomy

Introduction

The caddisfly family Sericostomatidae occurs in all biogeographic regions, except the Australasian, but its species diversity is very unevenly distributed across these regions (Morse 2010). Nineteen genera and 100 species have been described world wide, with half of the species occurring in the western Palearctic (50 species in 5 genera: Cerasma McLachlan, Notidobia Stephens, Oecismus McLachlan, Schizopelex McLachlan, Sericostoma Latreille) (Holzenthal et al. 2007b). South Africa harbors 12 species in 5 endemic genera (Aclosma Morse, Aselas Barnard, Cheimacheramus Barnard, Petroplax Barnard, Rhoizema Barnard), but no species are found in tropical Africa. The genus Agarodes Banks contains 12 species confined largely to the southeastern United States, where a second monotypic genus, Fattigia Ross, also occurs. There is a single species known from India, Asahaya asambaddha Schmid, and the 6 species in the genus Gumaga Tsuda occur in Mexico (Baja California) and the western United States (3 species) and in southern and eastern Asia (3 species). In the Neotropics, the family is represented in the Chilean subregion by 4 genera, Chiloecia Navás (1 species, nomen dubium), Myotrichia Schmid (1), Notidobiella Schmid (3), and Parasericostoma Schmid (10) (Flint et al. 1999b). Until now, only a single sericostomatid species, Grumicha grumicha (Vallot), was known from the Brazilian subregion (Flint et al. 1999a).

In this paper, we describe 3 new species of *Notidobiella*, 1 from the Amazon basin, Brazil, 1 from southeastern Brazil, and 1 from Ecuador, thus extending the range of this genus well beyond its Chilean representation. In addition, we provide illustrations and diagnoses of males and females (the latter for the first time) of the 3 previously described species of *Notidobiella*, *N. chacayana* Schmid, *N. inermis* Flint, and *N. parallelipipeda* Schmid, and a key to males of species in the genus. The Neotropical species of Sericostomatidae, including those in the genus *Notidobiella*, appear to be members of a southern Gondwana fauna (de Moor and Ivanov 2008).

Material and methods

Techniques and procedures used in the preparation and examination of specimens are those outlined by Blahnik and Holzenthal (2004) and Blahnik et al. (2007). Terminology for genitalia and wing venation follows that presented by Holzenthal et al. (2007b) and morphological structures are labeled in Figs 3–5. The species are presented in alphabetical order, except for the type species of the genus, *N. parallelipipeda*, which is presented first, after the generic diagnosis. Material examined and types are deposited in the collections of the University of Minnesota Insect Collection, St. Paul, Minnesota, USA (UMSP), the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP), the Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil (INPA), and the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (NMNH). UMSP barcode accession label numbers for holotypes are included in the list of material examined, but not for paratypes.

Systematics

Genus Notidobiella Schmid

Notidobiella Schmid 1955: 152 [Type species: *Notidobiella parallelipipeda* Schmid 1955, original designation].

Diagnosis: (modified from Schmid 1955; characters pertain to the male of the type species, except where noted): Head short, but broad, with large, projecting eyes, with conspicuous setae between ommatidea (Fig. 1); in most species interocular distance equal to or slightly less than diameter of eye, when viewed frontally (eyes of females smaller, interocular distance about 2× diameter of eye). According to Schmid (1955) bordering the eyes medially is an elongate, convex cephalic tubercle, but this structure was not evident in the material of the type species examined by us. Head dorsally with prominent, elongate occipital and retroccipital warts; ocellar, antennal, frontal, anterolateral, and hypomedial setal warts absent (terminology of Ivanov 1990) (although females with small anterolateral setal wart). Antennal scape much shorter than head and about as wide as long, with oval setal warts on both its dorsal and ventral surfaces; scapes almost touch medially. Maxillary palp very short, composed of enlarged, heavily setose basal article held against the face and sclerotized on its lateral side only, medial side membranous, with small, oval, sclerotized, setose apical article (Fig. 2) (female maxillary palp 5-segmented, unmodified). Labial palp 3-segmented, unmodified. Pronotum with pair of elongate setal warts (Fig. 1). Mesoscutum with very deep median fissure and pair of small, oval scutal warts; mesoscutellum with pair of large scutellar warts (Fig. 1). Each leg with pair of apical spurs (tibial spur formula 2-2-2). Wings are broad, forewing longer and broader than hind wing; wing venation uniform among the species. Forewing (Fig. 3A) with forks I, II, III, and V present; cross vein *r* between R1 and R2; discoidal cell present and short, forks II and III sessile; crossveins r-m and *m-cu* present (in *N. amazoniana* sp. n., and *N. ecuadorensis* sp. n., crossveins r and s absent or very weak and difficult to discern in the material examined; the absence of s leaves the discoidal cell open); Cu2 not attaining wing margin, merged apically with Cu1b; A1 and A2 each attaining wing margin, A3 absent. Hind wing (Fig. 3B) with discoidal cell open; forks I, II, V present; fork I petiolate; fork II sessile; M with single branch; fork V short. Male genitalia (Figs 4, 8): Sternum VII with posteromesal process. Segment IX with short or long ventral setose lobes or only single setose process (N. amazoniana sp. n.). Preanal appendages short, ovate, setose. Tergum X simple, triangular to subquadrate in shape. Inferior appendage narrow basally and broadly spatulate apically, with short to long mesal process on ventromesal margin (in N. amazoniana sp. n., inferior appendage uniformly narrow throughout its length and without mesal process on the ventromesal margin). Phallus simple, elongate, tubular, with prominent endophallic membranes. Female genitalia (Figs 5, 9): Tergum IX heavily setose, posterolateral lobe, with lateral, microsetose, elevated ridge (all species except N. brasiliana sp. n.). Internal vaginal sclerites complex with no discernable differences

among the species. Bursa copulatix subspherical and semisclerotized; pair of small, oval sclerites lying in membranes above vaginal sclerites (position variable).

Flint (1967) described the immature stages of *N. chacayana*. Larvae construct slightly tapered and curved cases of small mineral fragments embedded in silk and occur on the bottoms of small streams. The 3 previously known species, *N. chacayana* Schmid, 1957, *N. inermis* Flint, 1983, and *N. parallelipipeda* Schmid, 1955, are endemic to southern Chile.

Notidobiella parallelipipeda Schmid

Figs 1-5

Notidobiella parallelipipeda Schmid, 1955: 152 [Type locality: Chile, Nuble, Recinto; NMNH; male]. Flint 1974: 91 [distribution].

Description. Of the species in the genus with broad, spatulate inferior appendages (all species except *N. amazoniana*), the type species is the most distinctive based on the parallel-sided inferior appendages with their prominent, mesally directed, mesal processes.

Adult. Forewing length 7.8–8.0 mm male (n=2); 8.8–9.0 mm female (n=2). Color light brown, palps and legs stramineous; forewings light brown, with scattered golden setae. Sternum VII of male with broad, fingernail-like, posteromesal process.

Male genitalia (Fig. 4). Segment IX with anterior margin broadly produced midlaterally; tergum IX narrow; sternum IX with pair of very short, posteromesal processes, bearing long apical setae. Tergum X simple, subquadrate in lateral view, with slight apicolateral elevation, with slight dorsomesal excavation, setose apically. Preanal appendage short, ovate, setose. Inferior appendage prominent, heavily setose, spatulate, dorsal and ventral edges parallel, narrow basally, with prominent, elongate mesal process on mesal margin; strongly directed mesally in ventral view; apex exposed in lateral view. Phallic apparatus simple, tubular, slightly curved from base to apex; endophalic membranes prominent, but simple; phallotremal sclerite not apparent.

Female genitalia (Fig. 5). Tergum VIII quadrate; pleural membranes extensive, highly folded; sternum VIII broad, anterior margin with apodemal ridge, extending dorsolaterally; posterolateral corners rounded, heavily setose, especially posteriorly. Tergum IX with heavily setose, posterolateral lobes, rounded in lateral view, triangular in dorsal view; with lateral, microsetose, elevated ridge; sternum IX highly membranous, the membranes with parallel pleats or folds; tergum IX semimembranous dorsally. Tergum X with short setose projection. Internal vaginal sclerites complex (no discernable differences among the species); bursa copulatix subspherical, semisclerotized; pair of small, oval sclerites lying in membranes above vaginal sclerites (position variable).

Material Examined: CHILE: Nuble, Recinto, 4–6.iii.1968, Flint and Peña, 1 male, 1 female (pinned) (NMNH); Linares, El Castillo, Malcho, E Parral, 750 m, 8–10.i.1988, L.E. Peña, 1 male, 1 female (pinned) (NMNH).



Figures 1–3. *Notidobiella parallelipipeda* Schmid. I Male head and thorax **A** head, dorsal **B** pro- and mesonota, dorsal. **2.** *Notidobiella parallelipipeda* Schmid. Maxillary palp, male, frontal view. **3.** *Notidobiella parallelipipeda* Schmid. Male wings **A** forewing **B** hind wing. Abbreviations: DC = discoidal cell, TC = thyridial cell.



Figures 4–5. *Notidobiella parallelipipeda* Schmid. 4 Male genitalia A segments IX, X, inferior appendages, lateral B segments IX, X, dorsal C segment IX, inferior appendages ventral D inferior appendage, dorsal E phallus, lateral F phallus, ventral G sternum VII posteromesal process, ventral. 5. *Notidobiella parallelipipeda* Schmid. Female genitalia, segments IX, X, dorsal.

Notidobiella amazoniana Holzenthal & Blahnik, sp. n.

urn:lsid:zoobank.org:act:6203A2A2-CB58-418F-A731-8C31A2243E7D Figs 6–7

Description. This is the smallest species in the genus. Its wings are short and broad with venation typical for the genus except forewing crossveins *r* and *s* are absent, leaving the discoidal cell open (Fig. 7). Its genitalia are the most atypical in the genus in that the inferior appendages are not broadly spatulate, but sinuous in shape and uniform in width.



Figure 6. *Notidobiella amazoniana*, sp. n. Male genitalia **A** segments IX, X, inferior appendages, lateral **B** segments IX, X, dorsal **C** segment IX, inferior appendages ventral **D** phallus, lateral **E** apex of phallus, dorsal.

Tergum IX bears a short triangular, posteromesal process, rather than short, paired processes, as found in the other species. Otherwise, the genitalia are typical for the genus.

Adult. Forewing length 4.5–5.0 mm male (n=8). Color faded, overall pale stramineous (specimens in alcohol); forewings colorless, almost transparent, denuded. Sternum VII of male with broad, fingernail-like, posteromesal process.

Male genitalia (Fig. 6). Segment IX with anterior margin acutely produced ventrolaterally; tergum IX narrow, ridge-like; sternum IX with short, triangular, posteromesal process, bearing apical setae. Tergum X simple, subquadrate in lateral view, with slight dorsomesal excavation, setose. Preanal appendage short, ovate, setose. Inferior appendage prominent, heavily setose, elongate, narrow throughout length, without mesal process on ventromesal margin; in ventral view, apex acute, slightly incurved. Phallic



Figure 7. Notidobiella amazoniana, sp. n. Wings A forewing B hind wing.

apparatus simple, tubular, slightly curved from base to apex; endophalic membranes prominent, with paired apical membranous lobes; elongate, lightly sclerotized band internally (perhaps the phallotremal sclerite).

Female. Unknown.

Holotype male: BRAZIL: Amazonas: AM 010, km 246, 15–16.vii.1979, J. Arias (alcohol) (UMSP000131226) (INPA).

Paratypes: BRAZIL: Amazonas: same data as holotype, 3 males (alcohol) (UMSP), 4 males (alcohol) (NMNH).

Etymology: Named for the state and region where the specimens were collected, which represents a significant northern extension of the range of the genus.

Notidobiella brasiliana Holzenthal & Blahnik, sp. n.

urn:lsid:zoobank.org:act:3365A48E-060D-4925-AC4B-B8AD7E74944F Figs 8–10

Description. This new species is most similar to *N. chacayana* in the overall shape and structure of the inferior appendages. Both species possess an elongate mesal process on the ventromesal margin of the inferior appendage. In *N. ecuadorensis* sp. n., the ventromesal process is also present, but is shorter and broader in ventral view; in the other 2 Chilean species, *N. inermis* and *N. parallelipipeda*, the ventromesal processes are either very reduced (*N. inermis*) or long (*N. parallelipipeda*), but not nearly as long



Figure 8. *Notidobiella brasiliana*, sp. n. Male genitalia **A** segments VII-X, inferior appendages, lateral **B** segments IX, X, dorsal **C** segment IX, inferior appendages ventral **D** phallus, lateral **E** sterna VII, VIII, ventral.

as in *N. brasiliana* sp. n. Setting *N. brasiliana* sp. n., apart from all of its congeners is the pair of elongate posteromesal processes on sternum IX; in all other species these processes are much shorter and broader. Furthermore, forewing crossveins *r* and *s* are absent, leaving the discoidal cell open (Fig. 10).

Adult. Forewing length 7.0 mm male (n=1); 7.9–8.2 mm female (n=4). Color medium to dark brown, palps and legs light brown; forewings dark brown with scattered golden hairs, pale golden spot on anal margin at about midlength. Sternum VII of male with broad, fingernail-like, posteromesal process.

Male genitalia (Fig. 8). Segment IX with anterior margin broadly produced mesolaterally; tergum IX narrow, elevated, mound-like; sternum IX with pair of prominent, elongate, posteromesal processes, bearing long apical setae. Tergum X simple, triangu-



Figure 9. *Notidobiella brasiliana*, sp. n. Female genitalia **A** segments VIII-X, lateral **B** segments IX, X, dorsal **C** segments VIII-X, ventral.



Figure 10. Notidobiella brasiliana, sp. n. Wings A forewing B hind wing.

lar in lateral view, with slight dorsomesal excavation, setose. Preanal appendage short, ovate, setose. Inferior appendage prominent, heavily setose, broadly spatulate, narrow basally, with elongate mesal process on ventromesal margin. Phallic apparatus simple, tubular, slightly curved from base to apex; endophalic membranes prominent, but simple; phallotremal sclerite not apparent.

Female genitalia (Fig. 9). Tergum VIII quadrate; pleural membranes extensive, highly folded; sternum VIII broad, anterior margin with apodemal ridge, extending dorsolaterally; posterolateral corners rounded, heavily setose, especially posteriorly. Tergum IX with heavily setose, posterolateral lobes, rounded in dorsal and lateral views; without lateral ridge; sternum IX highly membranous, the membranes with parallel pleats or folds; tergum IX semimembranous dorsally. Tergum X with short, bifurcate, setose projection. Internal vaginal sclerites complex (no discernable differences among the species); bursa copulatix subspherical, semisclerotized; pair of small, oval sclerites lying in membranes above vaginal sclerites (position variable).

Holotype male: BRAZIL: São Paulo: Parque Estadual de Campos do Jordão, 1st order trib. to Rio Galharada, 22°41.662'S, 45°27.783'W, el 1530 m, 14–16.ix.2002, Blahnik, Prather, Huamantinco (pinned) (UMSP000086351) (MZUSP).

Paratypes: BRAZIL: São Paulo: Parque Estadual de Campos do Jordão, Rio Galharada, 22°41.662'S, 45°27.783'W, el 1530 m, 13–15.ix.2002, Blahnik, Prather, Melo, Huamantinco, 2 females (alcohol) (MZUSP); same data as holotype, 2 females (pinned) (UMSP).

Etymology: Named for Brazil, the country of the type specimens, which represents a significant northeastward extension of the range of the genus.

Notidobiella chacayana Schmid

Figs 11–12

Notidobiella chacayana Schmid 1957: 392 [Type locality: Chile, Maule, Chacay; NMNH; male]. Flint 1967:63 [larva, pupa]; 1974:91 [distribution].

Description. This Chilean species is most similar to *N. brasiliana* because of the similarly shaped inferior appendages, with their similar elongate mesal processes. It differs from that species in the much shorter posteromesal processes of sternum IX.

Adult. Forewing length 6.8–7.5 mm male (n=3); 7.2–9.0 mm female (n=3). Color brown, palps and legs stramineous; forewings brown, with scattered golden setae. Sternum VII of male with broad, fingernail-like, posteromesal process.

Male genitalia (Fig. 11). Segment IX with anterior margin produced ventrolaterally; tergum IX slightly elevated, mound-like; sternum IX with pair of short, posteromesal processes, bearing long apical setae. Tergum X simple, triangular in lateral view, with dorsomesal excavation, setose. Preanal appendage short, ovate, setose. Inferior appendage prominent, heavily setose, broadly spatulate, narrow basally, with elongate



Figures 11–12. *Notidobiella chacayana* Schmid. 11 Male genitalia A segments IX, X, inferior appendages, lateral B segments IX, X, dorsal C segment IX, inferior appendages ventral D phallus, lateral E phallus, ventral. 12. *Notidobiella chacayana* Schmid. Female genitalia, segments IX, X, dorsal.

mesal process on ventromesal margin. Phallic apparatus simple, tubular, curved from base to apex; endophalic membranes prominent, but simple; phallotremal sclerite not apparent.

Female genitalia (Fig. 12). Tergum VIII quadrate; pleural membranes extensive, highly folded; sternum VIII broad, anterior margin with apodemal ridge, extending dorsolaterally; posterolateral corners rounded, heavily setose, especially posteriorly. Tergum IX with heavily setose, posterolateral lobes, rounded to subtriangular in dorsal view; with lateral, microsetose, elevated ridge; sternum IX highly membranous, the membranes with parallel pleats or folds; dorsally tergum IX semimembranous. Tergum X with short setose projection. Internal vaginal sclerites complex (no discernable differences among the species); bursa copulatix subspherical, semisclerotized; pair of small, oval sclerites lying in membranes above vaginal sclerites (position variable).

Material Examined: CHILE: Cauquenes, Tregualeme, 35°56'S, 72°43'W, 11–12. xii.1993, C. and O. Flint Jr., 1 male, 1 female (pinned) (NMNH); X Región de los Lagos, Isla de Chiloé, Río Verde, 1.9 km W Puntra, 42°07.078'S, 73°50.364'W, el. 40 m, 3.ii.2005, Holzenthal, Blahnik, Chamorro, 2 males, 2 females (pinned) (UMSP); XIV Región de los Ríos, Monumento Nacional Alerce Costero, unnamed trib., trail to Alerce Milenario, 40°11.874'S, 73°26.217'W, el. 895 m, 5.ii.2008, Holzenthal, Pauls, Mendez, 1 male (pinned) (UMSP).



Figure 13. *Notidobiella ecuadorensis*, sp. n. Male genitalia **A** segments IX, X, inferior appendages, lateral **B** segments IX, X, dorsal **C** segment IX, inferior appendages ventral **D** inferior appendage, dorsal **E** phallus, lateral **F** phallus apex, dorsal **G** sternum VII posteromesal process, ventral.



Figure 14. Notidobiella ecuadorensis, sp. n. Wings A forewing B hind wing.

Notidobiella ecuadorensis Holzenthal & Blahnik, sp. n. urn:lsid:zoobank.org:act:20CB7DC2-73DF-4D4D-9593-0A87C589BABB Figs 13–14

Description. The combination of broadly spatulate inferior appendage, thumb-like mesal process on the ventromesal margin of the inferior appendage, and short posteromesal processes on sternum IX separate this species from its congeners. The wing venation (Fig. 14) is similar to that of the type species.

Adult. Forewing length 6.2 mm (n=1). Color faded, overall yellowish-brown (specimen in alcohol); forewings stramineous, denuded. Sternum VII of male with broad, fingernail-like, posteromesal process.

Male genitalia (Fig. 13). Segment IX with anterior margin broadly produced midlaterally; tergum IX narrow, elevated, mound-like; sternum IX with pair of short, triangular, posteromesal processes, bearing very long apical setae. Tergum X simple, triangular in lateral view, with slight dorsomesal excavation, setose apically. Preanal appendage short, ovate, setose. Inferior appendage prominent, heavily setose, very broadly spatulate, narrow basally, with short, thumb-like mesal process on ventromesal margin. Phallic apparatus simple, tubular, relatively straight from base to apex; endophalic membranes prominent, with paired apical membranous lobes; elongate, lightly sclerotized band internally (perhaps the phallotremal sclerite).

Female: Unknown.

Holotype: male, ECUADOR: Pastaza: Puyo, 1–7.ii.1976, Spangler et al. (alco-hol) (UMSP000208470) (NMNH).



Figures 15–16. *Notidobiella inermis* Flint. **15** Male genitalia **A** segments IX, X, inferior appendages, lateral **B** segments IX, X, dorsal **C** segment IX, inferior appendages ventral **D** phallus, lateral **E** phallus, ventral **F** sternum VII posteromesal process, ventral. **16.** *Notidobiella chacayana* Schmid. Female genitalia, segments IX, X, dorsal.

Etymology: Named for Ecuador, the country of the holotype, which represents a significant northern extension of the range of the genus.

Notidobiella inermis Flint

Figs 15-16

Notidobiella inermis Flint 1983: 90 [Type locality: Chile, Pcia Cautín, near Pucón; NMNH; male].

Description. Notidobiella inermis shares with N. ecuadorensis broadly spatulate inferior appendages with short, thumb-like mesal processes, but differs in details of the shape

of the inferior appendages, as illustrated, and in the possession of a narrow posteromesal process on sternum VII.

Adult. Forewing length 6.0–6.5 mm male (n=2); 8.0 mm female (n=2). Color brown, palps and legs stramineous; forewings brown, with scattered golden setae. Sternum VII of male with narrow, fingernail-like, posteromesal process.

Male genitalia (Fig. 15). Segment IX with anterior margin produced ventrolaterally; tergum IX narrow; sternum IX with pair of short, posteromesal processes, bearing long apical setae. Tergum X simple, subquadrate in lateral view, with slight dorsomesal excavation, setose. Preanal appendage short, ovate, setose. Inferior appendage prominent, heavily setose, very broadly spatulate, narrow basally, with short, thumb-like mesal process on ventromesal margin. Phallic apparatus simple, tubular, relatively straight from base to apex; endophalic membranes prominent, but simple; phallotremal sclerite not apparent.

Female genitalia (Fig. 16). Tergum VIII quadrate; pleural membranes extensive, highly folded; sternum VIII broad, anterior margin with apodemal ridge, extending dorsolaterally; posterolateral corners rounded, heavily setose, especially posteriorly. Tergum IX with heavily setose, posterolateral lobes, subovate, small, bilobed in dorsal and lateral views; with lateral, microsetose, elevated ridge; sternum IX highly membranous, the membranes with parallel pleats or folds; dorsally tergum IX with sclerotized ridge. Tergum X with broad heavily setose projection. Internal vaginal sclerites complex, no discernable differences among the species; bursa copulatix subspherical, semisclerotized; pair of small, oval sclerites lying in membranes above vaginal sclerites (position variable).

Material Examined: CHILE: Llanquihue, Salto Chamiza, Correntosa, 100 m, 19.i.1987, C.M. and O.S. Flint Jr., 1 male, 2 females (pinned) (NMNH); Llanquihue, El Chinque, N Correntosa (S Volcán Calbuco), 300 m, 20–25.i.1980, 1 male paratype (pinned) (NMNH).

Key to males of Neotropical Notidobiella

1	Inferior appendage narrow basally, broadly spatulate apically, with mesal pro-
	cess on ventromesal margin (Figs 4A, 8A); abdominal sternum IX with pair
	of posteromesal processes (Figs 4C, 8C); forewing length 6-8 mm2
_	Inferior appendage elongate, narrow throughout length, without mesal process
	on ventromesal margin (Figs 6A, C); abdominal sternum IX with single, short
	triangular, posteromesal process (Fig. 6C); forewing length 4.5-5 mm
	Notidobiella amazoniana sp. n
2(1)	Inferior appendage mesal process elongate (Figs 4C, 8C)
_	Inferior appendage mesal process short, thumb-like (Figs 13C, 15C)
3(2)	Posteromesal processes of abdominal sternum IX short (Figs 6C, 13C); distri-
	bution: Chilean subregion (Chile)4
_	Posteromesal processes of abdominal sternum IX elongate (Fig. 8C); distribu-
	tion: Brazilian subregion (southeastern Brazil) Notidobiella brasiliana sp. n

4(3)	Spatulate apex of inferior appendage broadly ovate (Fig. 11A)
	Notidobiella chacayana Schmid
_	Spatulate apex of inferior appendage parallel sided (Fig. 4A)
	Notidobiella parallelipipeda Schmid
5(2)	Abdominal tergum IX highly elevated, mound-like (Fig. 13A); ventromesal
	process of abdominal sternum VII broad (Fig. 13G); distribution: Brazilian
	subregion (Ecuador) Notidobiella ecuadorensis sp. n.
_	Abdominal tergum IX not elevated (Fig. 15A); ventromesal process of abdom-
	inal sternum VII narrow (Fig. 15F); distribution: Chilean subregion (Chile)
	Notidobiella inermis Flint

Biogeographic considerations

As defined most recently by de Moor and Ivanov (2008), the Trichoptera fauna of southern Chile and adjacent patagonian Argentina exhibits a strong biogeographical affinity to Australia, New Zealand, and other southern Pacific islands (e.g., New Caledonia). This "Temperate Gondwana" (de Moor and Ivanov 2008) or "transantarctic" pattern (e.g., Brundin 1966) also includes the temperate, southernmost part of Africa and Madagascar. In the Neotropical Trichoptera, the affinity to the southern African fauna is very weak, perhaps exhibited only at the family level within Sericostomatoidea (de Moor and Ivanov 2008) and potentially among genera within Sericostomatidae (although relationships among genera within this family are yet to be inferred). On the other hand, the biogeographical affinity between southern South America and Australasia is strong. Within South America, nearly all species in Chile and adjacent Argentina are endemic, prompting Flint (1976) to divide the Neotropics into 2 distinct subregions, the Chilean (southern Chile/Argentina) and the Brazilian (the rest of the Neotropics as defined by Wallace 1876); these regions are equivalent to the "Patagonian" and "Neotropical" (sensu stricto) Trichoptera regions of de Moor and Ivanov (2008).

Four Trichoptera families are representative of a temperate Gondwanan pattern: Helicophidae, Kokiriidae, Philorheithridae, and Tasimiidae, each family with genera endemic to Australia/New Zealand/New Caledonia, southern South America, or Madagascar (no genera are shared) (Neboiss 1986, Flint et al. 1999b, Holzenthal et al. 2007b, Weaver et al. 2008) (Table 1). Sukatcheva and Jarzembowski (2001) questionably placed a fossil (fragment of a forewing) from the early Cretaceous of southern England in the Helicophidae.

While not wholly endemic to the region, other caddisfly families contain a diverse temperate Gondwana fauna including, most notably, Hydrobiosidae (reviewed by Schmid 1989, Ward et al. 2004), Limnephilidae: Dicosmoecinae (Wiggins 2002) and Leptoceridae: Triplectidinae (Holzenthal 1986a, b, Morse and Holzenthal 1987, de Moor 1997, Holzenthal and Pes 2004, Calor et al. 2006, Calor and Holzenthal 2008, Malm and Johanson 2008). Other extant caddisfly taxa conforming to a tem-

Table 1. Genera (number of included species) in the families Helicophidae, Kokiriidae, Philorheithridae, and Tasimiidae and their regional distributions, including references to recent works inferring or discussing phylogenetic relationships among genera.

Family, genus (# species)	Distribution	
Helicophidae (Flint 1992, 2002, Henderson and Ward 2007, Johanson 2003a, Johanson and Keijsner		
2008, Johanson and Ward 2002, Neboiss 2002)		
Alloecella Banks (3)	SE Australia, Tasmania	
Alloecentrella Wise (4)	New Zealand	
Alloecentrellodes Flint (2)	Chile	
Austrocentrus Schmid (3)	Chile, Argentina	
Eosericostoma Schmid (2)	Chile, Argentina	
Helicopha Mosely (21)	Australia, Tasmania, New Caledonia	
Heloccabus Neboiss (1)	E Australia	
Microthremma Schmid (8)	Chile	
Pseudosericostoma Schmid (1)	Chile	
Zelolessica McFarlane (2)	New Zealand (incl. Stewart Island)	
Kokiriidae (Johanson 2003b)		
Kokiria McFarlane (1)	New Zealand	
Mecynostomella Kimmins (7)	New Caledonia	
Pangulia Navás (2)	Chile	
Tanjistomella Neboiss (1)	SE Australia	
Taskiria Neboiss(3)	SE Australia, Tasmania	
Taskiropsyche Neboiss (1)	Tasmania	
Philorheithridae (Henderson and Ward 2006, Weaver et al. 2008)		
Afrorheithrus Weaver, Gibon, and Chvojka (3)	Madagascar	
Aphilorheithrus Mosely (4)	SE Australia, Tasmania	
Austrheithrus Mosely (3)	SE Australia, Tasmania	
Kosrheithrus Mosely (3)	SE, SW Australia, Tasmania	
Mystacopsyche Schmid (2)	Chile, Argentina	
Philorheithrus Hare (6)	New Zealand	
Psilopsyche Ulmer (3)	Chile, Argentina	
Ramiheithrus Neboiss (2)	SE Australia, Tasmania	
Tasmanthrus Mosely (3)	Tasmania	
Tasimiidae (no phylogenetic assessment available)		
Charadropsyche Flint (1)	Chile	
Tasiagma Neboiss (2)	SE Australia, Tasmania, Lord Howe Island	
Tasimia Mosely (5)	SE Australia, Tasmania	
Trichovespula Schmid (1)	Chile	

perate Gondwanan pattern between the Neotropics (*sensu* Wallace) and Australasia include closely related or purported sister genera in otherwise more widely distributed or cosmopolitan families, including genera in Ecnomidae (Flint 1973, Li and Morse 1997, Cartwright 2009, Johanson and Espeland 2009), Hydropsychidae: Smicrideinae, Macronematinae (Neboiss 1984, Schefter 1996, Geraci et al. 2005), Philopotamidae (Blahnik 2005), and possibly Stenopsychidae. Other Trichoptera taxa endemic to

the Patagonian region (as defined by de Moor and Ivanov 2008), but that apparently either do not pertain to a transantarctic pattern or have unknown biogeographic affinities include genera in Anomalopsychidae (Holzenthal and Flint 1995, Holzenthal and Robertson 2006), Glossosomatidae (Robertson and Holzenthal 2005), Leptoceridae: Leptocerinae (Holzenthal 1986c), and Hydroptilidae (Harris and Armitage 1997, Harris and Flint 1993).

The family Sericostomatidae contains temperate Gondwanan components, including 5 endemic South African/Malagasy genera (*Aclosma, Aselas, Cheimacheramus, Petroplax, Rhoizema*) and 4 endemic South American genera (*Grumicha, Myotrichia, Notidobiella, Parasericostoma,* excluding *Chiloecia, nomen dubium*). As indicated above, the family includes other genera endemic to the Nearctic and West Palearctic regions. Sericostomatids are absent from the Australasian region (all Australasian species previously assigned to Sericostomatidae have been transferred to other families, see Holzenthal et al. 2007b for a historical review). Phylogenetic relationships among families and genera of Sericostomatoidea are largely unresolved (Holzenthal et al. 2007a) making it impossible to construct an area cladogram to test for congruence with the prevailing hypotheses of the geological sequence of the breakup of Pangea or the subsequent breakup of southern Gondwana (Sanmartín and Ronquist 2004, fig. 1).

The presence of Helicophidae and Hydrobiosidae in Eocene Baltic amber (Botosaneanu and Wichard 1983) and of fossil Plectrotarsidae (extant taxa endemic to Australasia) and a putative helicophid from late Cretaceous deposits in England (Sukatsheva and Jarzembowski 2001) suggests, as hypothesized by de Moor and Ivanov (2008), that certain southern temperate Trichoptera may be relicts of a more widespread fauna which included now extinct (but still extant in Sericostomatidae) north temperate elements. Two species of *Triplectides* in Baltic amber (Ulmer 1912) suggests the same scenario for this southern Gondwanan genus. In addition, the putative triplectidine larva from South Africa (de Moor 1997) and the recent discovery of Philorheithridae in Madagascar (Weaver et al. 2008) suggest at least a Gondwanan origin for these taxa (category 3 of Amorin et al. 2009) and, by inference, other endemic austral Trichoptera.

Evidence suggests that the contemporary distribution of the Patagonian and Australasian temperate Gondwanan Trichoptera fauna reflects a past dispersal corridor between Australia and southern South America via Antarctica (Sanmartín and Ronquist 2004). This "transantarctic exchange" pattern also has been demonstrated for other insects, including aquatic taxa (Cranston and Edward 1999, Amorin et al. 2009, Daugeron et al. 2009). However, it may be that the current distribution of other southern Gondwana caddisflies, such as Sericostomatidae, reflects an older dispersal prior to the breakup of southern Gondwana, now represented by relict Southern Hemisphere distributions. The southeast Brazilian sericostomatid *Grumicha grumicha* might represent evidence to support the relict hypothesis.

The now widespread occurrence of *Notidobiella* in temperate southern Chile and tropical South America (Ecuador, southeast Brazil, Amazonian Brazil) suggests a more recent dispersal of the genus to northern tropical South America from Patagonia and

its subsequent diversification. The data from insects analyzed by Sanmartín and Ronquist (2004, table 4) found a significantly higher frequency of dispersal from southern South America to northern South America than from the other direction. This may be true for other caddisflies with both Patagonian and Neotropical (*sensu* de Moor and Ivanov) distributions, including *Antarctoecia* (Huamantinco and Nessimian 2003), *Atopsyche* and *Cailoma* (Hydrobiosidae) (Ross and King 1952, Flint 1974, Schmid 1989 [although *Atopsyche* is absent from Patagonia, its putative sister genus is Patagonian]), *Contulma* (Anomalopsychidae) (Holzenthal and Flint 1995), *Smicridea* (*Smicridea*) (Hydropsychidae) (Flint 1989), *Tolhuaca* (Glossosomatidae) (Robertson and Holzenthal 2005), and *Triplectides* (Leptoceridae).

As confirmed by Crisci et al. (1991), Sanmartín and Ronquist (2004), and Amorin et al. (2009) the historical biogeography of southern South America is complex. The distribution of the austral South American caddisflies support this conclusion, with a fauna pertaining strongly to a transantarctic pattern, but with perhaps older Gondwana elements, as exhibited by Sericostomatidae. The current weight of evidence described above, however, supports a more recent dispersal of this southern fauna to northern South America.

Other than in a few studies, phylogenetic hypotheses are lacking for most of the taxa reviewed above. Phylogenies of Southern Hemisphere caddisfly taxa inferred from molecular data are even fewer (e.g., Johanson and Keijsner 2008) and only one (Johanson et al. 2009) has used events-based models (e.g., Sanmartín at al. 2001, Ronquist and Sanmartín 2004) or divergence time estimates (but see Amorin et al. 2009 for a critique of molecular dating) to address historical biogeography. Given the current ease with which molecular sequence data can be obtained and with the availability of newer analytical methods (e.g., Ronquist 1997, Sanderson 2002, Zaldivar-Riverón et al. 2008), there is a wealth of hypotheses that can be tested regarding the historical biogeography of the austral caddisfly fauna once phylogenetic information is available (Santos and Amorin 2007).

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RESEARCH ARTICLE



A revision of the genus Antepione Packard with description of the new genus Pionenta Ferris (Lepidoptera, Geometridae, Ennominae)

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Abstract

Based on genitalic studies, the new genus *Pionenta* is established for two taxa formerly placed under *Antepione*. The taxa *hewesata* and *ochreata* (and previously associated synonyms) are now synonomized as *Pionenta ochreata*. Three species of *Antepione* are now recognized: *A. thisoaria*, *A. imitata*, *A. tiselaaria* with the taxa *comstocki*, *constans*, and *indiscretata* synonomized under *A. imitata*. No new species are described. Adults and genitalia are illustrated, including type specimens.

Keywords

Antepione, Arizona, Colorado, Costa Rica, Ennominae, Geometridae, Guatemala, Lepidoptera, Mexico, New Mexico, nomenclature, North America, *Pionenta*, taxonomy, Texas

Introduction

A genitalic study of the eight species recognized by Parsons et al. (1999) associated with genus *Antepione* uncovered two distinct and quite different forms in both the male and female genitalia. This situation was alluded to by Pitkin (2002: 283), who excluded *Antepione ochreata* (Hulst) in her treatment of the genus. In *Antepione*, as restricted herein, the

Copyright *Clifford D. Ferris*. This is an open access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. male genitalia lack a furca, and the female genitalia lack a signum. I recognize three species of *Antepione. Antepione thisoaria* (Guenée) is widely distributed in eastern North America with additional records for Mexico, Guatemala and Costa Rica. *A. imitata* occurs in the southwestern United States from Texas to Arizona. *A. tiselaaria* (Dyar) ranges from central Mexico to Costa Rica. In the genus *Pionenta*, as subsequently described, I recognize only one species, *P. ochreata*. The male genitalia have a stubby robust furca, and the female genitalia a single large stellate signum. The species assigned to both genera are sexually dimorphic and extremely polyphenic, which, lacking genitalic examination, historically apparently led to the descriptions of multiple taxa. My field collections of multiple specimens in ultraviolet light traps at single sites and subsequent genitalic dissections allowed me to assess variation. The range of *Pionenta* is southwestern New Mexico and southeastern Arizona. It most likely occurs in contiguous northern Mexico, but I have found no records.

Materials and Methods

Repository abbreviations

AMNH	American Museum of Natural History, New York, NY, USA.
ANSP	Academy of Natural Sciences, Philadelphia, PA, USA.
BMNH	The Natural History Museum (formerly British Museum [Natural Histo-
	ry]), London, UK.
CDF	Personal collection of Clifford D. Ferris, Laramie, WY, USA.
CMNH	Carnegie Museum of Natural History, Pittsburgh, PA, USA.
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Ot-
	tawa, Ontario, Canada.
EME	Essig Museum of Entomology, University of California, Berkeley, CA, USA.
FMNH	Field Museum of Natural History, Chicago, IL, USA.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA,
	USA.
MNHN	Museum National d'Histoire Naturelle, Paris, France.
SEM	Snow Entomological Museum Collection, University of Kansas, Lawrence,
	KS, USA.
USNM	National Museum of Natural History [formerly United States National
	Museum], Washington, District of Columbia, USA.

Methods and general terminology. Terms for genital structures and wing markings follow Ferris and Schmidt (2010).

Description abbreviations

AML	Antemedial line.
DFW	Dorsal forewing.

Dorsal hindwing.
Forewing length, measured along costa from base to apex.
medial band = area between DFW AML and PML.
Postmedial line.

TL Type locality.

Key to genera

(based on DFW pattern and genitalia)

- DFW triangular costal dark patch absent; male genitalia with robust stubby furca; female genitalia with colliculum and signum........ *Pionenta ochreata*

Key to Antepione species

(based on genitalia)

1	Male genitalia: apical region of valva lacks spines. Female genitalia: corpus
	bursa oblong and initially swollen with membranous anterior sac thisoaria
_	Not as above
2	Male genitalia: valva rounded at apex with 3 long robust spines and addi-
	tional fine setae. Female genitalia: corpus bursae long and cylindrical with
	membranous anterior sac imitata
_	Not as above
3	Male genitalia: valva rounded at apex with multiple short slender translucent spines over most of surface excepting toward base. Female genitalia unknown to author

Antepione Packard, 1876: 459, 483

Type species: *Epione depontanata* Grote, 1864. Location of type unknown; originally placed in ANSP. Described from Maryland, USA.

Mimogonodes Warren, 1895

Type species: Mimogonodes constricta Warren, 1895 [BMNH].

Diagnosis. Adults. Medium sized (FWL 13–21 mm) basically ochreous-colored moths with variable markings on DFW. DFW outer margin angulate at vein M₃. Separation from similar genera is by the combination of characters: filiform anten-

nae; male genitalia with stout tapered decurved uncus, valvae with even outer margins lacking projections, absence of furca; female genitalia without colliculum and signum.

Description. Adults. Sexually dimorphic and sexes polyphenic; FWL 13-21 mm. Antenna simple, more slender in females. *Head* – Dark ochreous speckled with darker scales, concolorous collar; labial palpi broad, barely extending beyond frons, ochreous speckled with darker scales. Thorax, abdomen, legs - Ochreous or pale tan as in wings with widely scattered small brown scales. Wings - FW outer margin arcuate at vein M₃ and HW; DFW apex acute to falcate. Usually obscure narrow dark DFW submarginal band; small dark discal spots both wings. Males. Dorsal color varies from gray, medium ochreous to medium brown. DFW AML and PML variable from pronounced and dark to broken and indistinct; medial band concolorous with remainder of wing, or paler and yellowish; a dark triangular patch with blunted or acute apex, with or without pale oblong spot, located along costa distad of PML. DHW with dark narrow medial band varying individually from dark to indistinct. Ventrally paler with dorsal maculation repeated, usually with less intensity. Females. Dorsal color varies from yellow through pale ochreous to medium ochreous and gray. Crosslines usually indistinct. DFW triangular patch as in males, PML above inner margin expanded into two large oblong brown spots. Ventrally paler with dorsal maculation repeated, usually with less intensity. Male genitalia - Uncus stout, slightly decurved, tapering to a rounded tip; medial gnathos with a few small teeth; valva rounded at apex; anellus with small spines; aedeagus truncate with one large oblong cornutus near base of vesica. Female genitalia – Apophyses long, slender; posterior apophyses ca. 1.8 × anterior apophyses; colliculum absent; ductus bursae ridged, short, partially sclerotized at posterior end; corpus bursae without signum, oblong with membranous anterior sac; ductus seminalis originates at top of ductus bursae.

Remarks. McDunnough (1938) treated *Epione depontanata* and *Heterolocha sulphurata* Packard, 1876 as synonyms of *Hyperythra arcasaria* Walker, 1860. Forbes (1948:108) placed *Hyperythra arcasaria* as a synonym of *Heterolocha thisoaria* [Guenée, 1858], which he then placed as *Sabulodes thisoaria*, and lumped several genera, including *Antepione*, under *Sabulodes* Guenée [1858]. Subsequent authors (Ferguson, 1983; Covell, 1984; McGuffin, 1987) restored *Antepione* as a separate genus. Ferguson recognized the species: *comstocki* Sperry; *hewesata* Sperry; *imitata*, H. Edwards.; *indiscretata*, (H. Edwards); *ochreata* (Hulst); *thisoaria* (Guenée); *tiselaaria* (Dyar). The geographic range of the genus includes eastern North America, the southwestern United States, portions of Mexico, Costa Rica and Guatemala.

Systematics

Antepione thisoaria (Guenée, 1857 [1858]) Figs 1, 11–19, 59

Antepione sulphurata Packard 1876: 484 *Epione depontanata* Grote 1864: 90 *Eutrapela furciferata* Packard 1876: 559 *Gonopteryx rhomboidaria* Oberthür 1912: 246, pl. 148, f. 1401 *Heterolocha sulphurata* Packard 1873: 79 *Heterolocha thisoaria* Guenée 1857 [1858]: 106. *Hyperythra arcasaria* Walker 1860: 131 *Mimogonodes constricta* Warren 1895: 149 *Sabulodes thisoaria* Forbes 1948: 108 *Tetracis azonax* Druce 1892: 54, pl. 46, f. 8 *Tetracis rivulata* Warren 1897: 506

Type material. Female HT (Fig. 1), country of origin not stated [MNHN].

Fixation of type locality. The Central American taxa were not recognized and described until 1892 (*azonax*) and 1912 (*rhomboidaria*). On this basis, I infer that specimens from this region were not available to Guenée in 1857 when he described *thisoaria*, and that the holotype was collected in eastern North America. In habitus, the HT matches exactly female specimens of the *sulphuraria/sulphurata* form. The HT was most probably collected in the Middle Atlantic region. I hereby fix the type locality as eastern North America. Based on my research, it appears that Forbes (1948) was the first to use the name *thisoaria* in the North American fauna.

Other material examined. 84 specimens (a few by photograph) from Alabama, Indiana, Kentucky, Mexico, Michigan, New Jersey, New York, Nova Scotia, Pennsylvania, Quebec, Tennessee, Virginia. Additional distribution records were obtained from individuals and several museums, including 439 from the Carnegie Museum of Natural History, Pittsburgh, PA.

Diagnosis. *Antepione thisoaria* is most easily separated from *A. imitata* based on geography. It does not occur west of the 95th parallel, while *A. imitata* extends eastward only to west Texas, and is not recorded from Central America. In the male genitalia, the apical region of the valva lacks spines, which are present in the valva of *imitata*. In the female genitalia, the corpus bursae is initially swollen while not so in *A. imitata*.

Description. Adults. As described above for the genus. **Genitalia.** Figs 17–19. Two dissections (male and female) by author; illustrations in McGuffin (1987, Figs 242g, 245e); Pitkin (2002, Figs 202, 460). *Male genitalia* – Uncus stout, slightly decurved, tapering to a rounded tip; gnathos with unjoined slender arms, medial gnathos with a few small teeth; valva rounded at apex without spines, produced ventral ridge forming two short projections; anellus with two sclerotized spinose lobes; aedeagus truncate with one large narrow elliptical cornutus near base of vesica. *Female genitalia* – Apophyses long, slender; posterior apophyses ca. 1.8 × anterior apophyses; ductus bursae ridged, moderately short, partially sclerotized at posterior; corpus bursae without signum, corpus bursae without signum, oblong and initially swollen with membranous anterior sac; ductus seminalis originates at top of ductus bursae.

Biology and distribution (Fig. 59). McGuffin (1987: 88–89) described the early stages and cited three specific larval hosts: *Alnus rugosa* (Du Roi) Spreng; *Physocarpus opulifolius* (L.) Maxim; *Prunus serotina* Ehrh. Various additional larval hosts are report-



Figures 1–4. *Antepione* species. **I** *A. thisoaria* HT (dorsal and ventral) with pin labels (MNHN photo) **2** *A. imitata* HT with pin labels (SEMC photo) **3** *A.* (*Tetracis*) *indiscretata* HT with pin labels (SEMC photo) **4** *A.* (*Eugonobapta*) *constans* HT, adult, pin labels (AMNH photo) and male genitalia. The balsam embedding medium has fogged with age producing the apparent lack of focus in the genitalia photo.

ed in the literature in the families Aceraceae, Anacardiaceae, Betulaceae, Ebenaceae, and Rosaceae. The last instar larva was illustrated by Wagner et al. (2001, p. 155) and Wagner (2005, p. 195). Adults fly April–May with an occasional mid-March and mid-June record, July–August with occasional September to mid-October records. There is

one generation in Canada, and at least two southward. The distribution map (Fig. 59) represents the data that I was able to locate. The heavy distribution in Pennsylvania reflects intensive collecting in that state by CMNH personnel and volunteers. Undoubtedly similar efforts in neighboring areas should produce additional records. The overall range of this species is: in CANADA from Nova Scotia to Manitoba; in the UNITED **STATES** (county records in parentheses) then south and west to the Gulf states to the 95th parallel, including Alabama (Bibb, DeKalb, Jackson, Madison, Monroe), Arkansas (Logan, Montgomery, Polk, Scott, Washington), Connecticut (Fairfield, Hartford, New Haven, New London, Tolland, Windham), Georgia (Cherokee, Rabun), Illinois (Cook, Macon), Indiana (Elkhart, Jackson, Jasper, Lagrange, Laporte, Monroe, Newton, Perry, Pulaski, St. Joseph), Iowa (Johnson, Monroe), Kansas (Crawford), Kentucky (Bell, Boone, Bracken, Bulitt, Calloway, Carter, Fayette, Graves, Harlan, Jefferson, Madison, McCracken, Meade, Menifee, Metcalfe, Morgan, Muhlenberg, Oldham, Owsley, Powell, Rowan, Russell, see Covell, 1999), Louisiana (Feliciana Parish), Maine (Aroostook, Franklin, Oxford, Penobscot, Piscataquis), Maryland (Allegheny, Anne Arundel, Baltimore, Cecil, Garrett, Harford, Howard, Washington, Worcester), Massachusetts (Berkshire, Dukes, Essex, Middlesex, Nantucket), Michigan (Berrien, Cass, Otsego), Minnesota (Houston), Mississippi (Franklin, George, Grenada, Harrison, Kemper, Lee, Marshall, Oktibbeha, Pike, Pontotoc, Tishomingo, Union, Warren, Webster, Winston), Missouri (Barry, Benton, Camden, Cape Girardeau, Carter, Greene, Jasper, Lafavette, Lewis, Madison, Morgan, Newton, Stoddard, Warren, Wayne), Nebraska (Cass), New Jersey (Burlington, Essex, Gloucester, Morris, Passaic, Sussex, Union, Warren), New Hampshire (Rockingham), New York (Albany, Kings, Queens, Nassau, Suffolk, Westchester), North Carolina (Allegheny, Ashe, Avery, Stokes, Swain, Transylvania), Ohio (Adams, Ashland, Ross, Wayne), Oklahoma (Cherokee, see Nelson, 2010), Pennsylvania (Adams, Allegheny, Armstrong, Beaver, Bedford, Berks, Blair, Bucks, Butler, Centre, Chester, Clearfield, Crawford, Dauphin, Fulton, Greene, Huntingdon, Lawrence, Northumberland, Perry, Somerset, Washington, Westmoreland, York), Rhode Island (Washington), South Carolina (Greenville), Tennessee (Louden, Wilson), Virginia (Augusta, Carroll, Giles), West Virginia (Cabell, Grant, Greenbrier, Hampshire, Mason, Monongalia, Monroe, Pendleton, Randolph, Roane, Wyoming); MEXICO (Michoacan state); CENTRAL AMERICA in Costa Rica and Guatemala (Pitkin et al. 1996). Covell (1984) stated the westward range of the species to Texas. I have been unable to confirm Texas from museum records. Forbes (1948) stated: ". . . varieties in Colorado, Texas, and Arizona." His "varieties" are assumed to be A. imitata. Although the distribution map (Fig. 59) suggests occurrence of thisoaria in Florida, Vermont and Wisconsin, no records were found.

Remarks. The gray spring form of the moth (Figs 11, 15) was described by Packard as the species *furciferata*. The male (Fig. 14) represents the summer form *arcasaria*, and the female (Fig. 16) represents the summer form *sulphuraria* = *sulphurata*. Packard (1876) redescribed *Heterolocha sulphuraria* Packard, 1873 as *Antepione sulphurata*. Once barcoding data are available, the disjunct distributions of Mexican and Central American populations may ultimately prove to be separate species, in which case the

name *azonax* Druce, 1892 (Costa Rica, Guatemala) is available and has date priority over *rhomboidaria* Oberthür, 1912 (Costa Rica) and *rivulata* Warren, 1897 (Costa Rica). The two female specimens in the CNC from Tuxpan, Michoacan, Mexico are exact matches for the *sulphurarialsulphurata* phenotype and were collected in early August, 1959.

Antepione imitata Edwards, 1884

Figs 2-5, 20-33, 59

Antepione comstocki Sperry 1939, syn. n. Antepione costinotata Taylor 1905 Eugonobapta constans Hulst 1898, syn. n. Metanema vanusaria Strecker 1899: 6, syn. rev. Tetracis indiscretata Edwards 1884: 48, syn. n.

Type material. Female HT (Fig. 2), New Mexico, [San Miguel Co.], Las Vegas, July, 1882. [SEMC].

Antepione comstocki male HT (Fig. 5), Arizona, [Pima Co.], Baboquivari Mts., 26 April, 1938 [CNC]. *Tetracis indiscretata* female HT (Fig. 3), New Mexico, [San Miguel Co.], Las Vegas, August, 1882 [SEMC]. *Eugonobapta constans* male HT (Fig. 4), Arizona, [Yavapai Co.], Prescott, August, 1896 [AMNH].

Other material examined. 145 specimens in [CDF] from Arizona, Colorado and New Mexico; additional material (some by photographs) from Arizona (including a reared series), Colorado, New Mexico, Texas, Mexico.

Diagnosis. Antepione imitata is most easily separated from *A. thisoaria* based on geography. It does not occur east of west Texas and is not recorded from Central America, while *A. thisoaria* extends west only to the 95th parallel. In the male genitalia, the apical region of the valva exhibits 3 long robust spines and additional fine setae, which are not present in the valva of *thisoaria*. In the female genitalia, the corpus bursae is not initially swollen as in *A. thisoaria*.

Description. Adults. As described above for the genus. **Genitalia.** Figs 4, 31–33. Dissections 8m, 2f comprising full range of phenotypes). *Male genitalia* – Uncus stout, slightly decurved, tapering to a rounded tip; gnathos with unjoined slender arms, medial gnathos with a few small teeth; valva rounded at apex with 3 long robust spines and additional fine setae, produced ventral ridge forming two short projections; anellus with two sclerotized spinose lobes; aedeagus truncate with one large oblong cornutus near base of vesica. *Female genitalia* – Apophyses long, slender; posterior apophyses ca. 1.8 × anterior apophyses; ductus bursae ridged, short, partially sclerotized at posterior; corpus bursae without signum, long and cylindrical with membranous anterior sac; ductus seminalis originates at top of ductus bursae.

Remarks. One male specimen (Fig. 25) of the *comstocki* phenotype examined from Las Animas Co., Colorado lacks the characteristic DFW costal triangular patch, caus-



Figures 5–10. Antepione species. 5 A. comstocki HT with pin labels (CNC photo) 6–10 A. tiselaaria. 6 HT with pin labels (USNM photo) 7–8 adult males 9 male genitalic capsule, aedeagus removed 10 aedeagus with vesica everted.

ing it to resemble superficially the *ligata* form of *Pionenta ochreata*. The male genitalia, however, are typical of *A. imitata*.

Biology and distribution (Fig. 59). Noel McFarland (Hereford, AZ) reared the species on *Ribes aureum* Push. from ova from an adult female of the nearly uniformly brownish-ochreous April–May generation; adults emerged June–July. The



Figures 11–19. *Antepione thisoaria*. 11–14 adult males 15–16 adult females 17 male genitalic capsule, aedeagus removed 18 aedeagus with vesica everted 19 female genitalia.

resulting adults are of the form with yellow females and males in which the DFW medial band has a yellow flush. Based on my field studies over many years in southeastern Arizona and southwestern New Mexico and McFarland's reared material, there appear to be three generations in southeastern Arizona and Southwestern New Mexico. There is a strong early flight starting in April and early May, with a weaker flight in late June into July, and another strong flight beginning in mid-August after the monsoonal rains with a few individuals into early October. This species ranges from west **Texas** (Brewster, Culberson, Jeff Davis), **Colorado** (Delta, La Plata, Las



Figures 20-30. Antepione imitata adults. 20-25 males 26-30 females.

Animas), New Mexico (Grant, Harding, Hidalgo, San Miguel), to southern Arizona (Cochise, Gila, Pima, Santa Cruz). A typical male specimen was examined [CMNH] with the collection data: Mexico: Coahuila, Sierra La Madera, upper Canada Desiderio, 15–17 March 1985, 27–08N, 102–31W, 1810m, J. Rawlins, S. Thompson. This locality is essentially due south of the western Texas records, and one might anticipate that with further collecting *A. imitata* will prove to be widespread in northern Mexico. It is generally associated with riparian canyons up to 6000' (1830m).

Discussion. As is also the case with *Antepione thisoaria*, most spring individuals of *A. imitata* are rather drab in appearance with lightly maculated brownish males (the *comstocki* phenotype) and pale creamy colored or ochreous females. The strongly maculated males and yellow females appear in the later generations in company with



Figures 31–33. *Antepione imitata* genitalia. 31 male genitalic capsule, aedeagus removed 32 aedeagus with vesica everted 33 female genitalia.

the rather drab early-season phenotypes. In his original descriptions of *imitata* and *indiscretata*, Edwards provided no insight as to why he assigned *imitata* to *Antepione* and *indiscretata* to *Tetracis*. Both taxa are described on the same page with the description of *imitata* preceding that of *indiscretata*. He characterized the color of *imitata* as similar to the yellow *sulphurata* phenotype of *thisoaria*, and *indiscretata* as "Ochraceus drab." Over the years the type specimens have faded to some extent so that they now appear nearly identical in color, the only difference being the extent of the dark maculation. The name *constans* appears to have been applied to the heavily maculated male phenotype, as best can be determined from the poor condition of the HT.

Antepione tiselaaria (Dyar, 1912) Figs 6–10

Paragonia tiselaaria Dyar 1912

Type material. Male HT (Fig. 6), Mexico, Minerale de Zacualpan, January, 1911 [USNM]. Comment: Dyar (1912: 87) stated the type locality only as "Zacualpan" and



Figures 34–39. Pionenta ochreata. 34 P. ochreata HT with pin labels (AMNH photo) 35 P. (Antepione) hewesata HT with pin labels (AMNH photo) 36–37 P. (Sabulodes) ligata 36 HT with pin labels 37 genitalia 38 P. (Sabulodes) arizonata HT with pin labels 39 P. (Sabulodes) dyari HT with pin labels. (36–39 USNM photos).

not "Minerale de Zacualpan" as shown on the specimen label. I interpret the label to mean the Zacualpan mining region located in the state of Morelos south of Mexico City, today still an active silver mining district.

Other material examined (Figs 7–10). MEXICO. Puebla, 2 mi. SW Tehuacan, 5300', 4.x.1975, Powell (1m, dissected); same, 5.x.1975, J. Powell (1m) [EME].

Diagnosis. Females not known to the author. Mexican specimens of *Antepione tise-laaria* males are most easily separated from *A. imitata* based on geography, since the latter species does not penetrate south to central Mexico. In Costa Rica, where *A. thisoaria* is also



Figures 40-53. Pionenta ochreata adults. 40-48 males 49-53 females.

reported, *A. tiselaaria* manifests a more orange-brown overall color than the drab ochreousgray form of *thisoaria*. In the male genitalia, the apical region of the valva is covered with multiple short slender translucent spines over most of the surface except toward the base; spines are absent in the valva of *A. thisoaria*, and 3 long robust spines occur in *A. imitata*.

Description. Adults. Only males were available for examination. As described above for the genus, other than the wings. FWL 17–18 mm. *Wings* – FW outer margin arcuate (roundly produced about) vein M₃ and HW; DFW apex sightly acute, not fal-

cate. Dorsal color pale orange-brown-ochreous with darker maculation. AML a narrow band centrally with a few paler scales, PML an interrupted band with irregular edges and centrally paler, widening substantially approaching inner margin; MB not clearly defined with splotchy brown maculation over paler ground color; a dark triangular patch with blunted or acute apex, with or without pale oblong spot, located along costa distad of PML; small dark discal spots FW and HW. Ventrally paler with dorsal maculation repeated with slightly less intensity. **Male genitalia.** Figs 9–10. Dissection 1m. Uncus stout, slightly decurved, tapering to a rounded tip; gnathos with unjoined slender arms, medial gnathos with a few very small dark teeth; valva rounded at apex with multiple short slender translucent spines over most of the surface excepting toward the base, produced ventral ridge forming one large and one short projection; anellus with two sclerotized spinose lobes; aedeagus truncate with one large (equal to diameter of aedeagus shaft) oblong triangular cornutus near base of vesica; fully everted vesica initially spherical becoming a tapered tube.

Biology and distribution. Early stages unknown. Current distribution records are for the Mexican states of Morelos and Puebla, and Costa Rica.

Pionenta Ferris, gen. n.

urn:lsid:zoobank.org:act:95BF80CA-F55F-40D9-B877-A25252635770

Type species: Antepione ochreata Hulst, 1898.

Etymology. *Pionenta* is a masculine anagram of *Antepione*.

Diagnosis. *Pionenta ochreata* lacks the DFW triangular costal patch found in all species of *Antepione*. The well-developed DFW AML and PML form a wedge-shaped medial band absent in *Antepione*. The robust centered furca in the male genitalia and large stellate signum in the female genitalia of *Pionenta* are absent in *Antepione*.

Description. Adults. Sexually dimorphic and both sexes are polyphenic; FWL 14-19 mm. Antenna simple. Head - Uniformly ochreous, collar concolorous; labial palpi relatively narrow, slightly upcurved, ochreous, barely extending beyond frons. Thorax, abdomen, legs - Uniformly colored as in ground color of wings with a few widely scattered small brown scales on legs. Wings - Outer margin arcuate FW (about M3) and HW; DFW apex normally sightly falcate. Wing color variable from pale creamy white to ochreous tan. AML and PML narrow and brown (occasionally reddish-brown), PML continues on DHW as medial line; AML with narrow pale shading basad, PML with narrow pale shading distad. MB trapezoidal tapering inward from costa to inner margin. Small dark discal spots present FW and HW. Scattered dark patches may be present basally and submarginally on DFW, and submarginally on DWH. Ventrally paler with dorsal maculation only weakly repeated. Male genitalia (7 dissections by author, additional museum slides examined) - Uncus stout, slightly decurved, tapering at apex to a rounded tip; gnathos v-shaped with well-sclerotized edges, medially a sharp upcurved tip with numerous very small teeth; valva rounded at apex, but with blunt triangular projection at end of sclerotized costa;



Figures 54–58. *Pionenta ochreata* genitalia. **54–57** male genitalic capsules, adeagii removed and adeagii with vesicas everted (arrows point to deciduous setae) **58** female genitalia.

anellus membranous without spines or setae, with central robust cylindrical furca covered by numerous short spines on rounded apex; aedeagus truncate with two long sclerotized pointed extensions from apical margin and a variable patch of apparently deciduous dark setae near base of otherwise membranous short cylindrical vesica. *Female genitalia* (6 dissections) – Posterior apophyses short, anterior apophyses much



Figure 59. Partial distribution map for Antepione thisoaria and A. imitata.



Figure 60. Distribution map for *Pionenta ochreata* (counties only).

reduced ca. $0.4 \times$ posterior apophyses; sterigma well sclerotized; posterior margin of lamella antevaginalis rounded at ends with central depression; well-defined colliculum; partially ridged short ductus bursae opens into ovoid membranous corpus bursae; one large centrally located oval stellate signum; ductus seminalis originates immediately below colliculum.

Pionenta ochreata Hulst, 1898

Figs 34-58, 60

Antepione hewesata Sperry 1948, syn. n. Sabulodes arizonata Taylor 1905, syn. rev. Sabulodes dyari Grossbeck 1908, syn. rev. Sabulodes ligata Grossbeck 1908, syn. rev.

Type material. Male HT (Fig. 34), Arizona, Senator [probably Senator Mine, Yavapai Co.] [AMNH].

Antepione hewesata female HT (Fig. 35), Arizona [Coconino Co.], Oak Creek Canyon, Todd's Lodge, [AMNH]. Sabulodes arizonata male HT (Fig. 38), Arizona [Cochise Co.], Huachuca Mts. [USNM]. Sabulodes dyari male HT (Fig. 39), Arizona [Cochise Co.], Huachuca Mts. [USNM]. Sabulodes ligata male HT (Figs 36–37), Arizona [Cochise Co.], Huachuca Mts. [USNM].

Other material examined. 135 specimens in [CDF] from Arizona and New Mexico; 61 additional specimens (some by photographs) from Arizona.

Diagnosis. As for genus.

Description. General description as for genus.

Remarks. Antepione ochreata has two distinct phenotypes. The male form with pale ochreous wing color and varying numbers of multiple dark patches (Figs 34, 40–43) was described as ochreata. The female described as hewesata (Figs 35, 44) is intermediate between typical ochreata and the brownish-tan phenotype without dark patches described as ligata (Figs 36, 46, 50–53) which is the usual female form based on my field experience and examination of museum material. Regarding the taxa arizonata and dyari, apparently some years ago an accident occurred with a drawer containing type specimens and they were badly damaged. Figs 38 and 39 illustrate what remains of these two specimens. Their associated genitalia slides were not damaged and the preparations agree with Figs 37, 54–57.

Biology and distribution (Fig. 60). Early stages unknown. Adults from mid-May to August in riparian canyons and dry coniferous forest to 8400' (2560m); probably more than one generation. Collection records include **Arizona** (Cochise, Coconino, Pima, Santa. Cruz, Yavapai), **New Mexico** (Grant).

Discussion. Based on the male and female genitalia, *Pionenta* is closely related to *Tetracis*. The male genitalia of both genera possess a well defined central furca. The female genitalia of both genera possess a well defined colliculum and prominent single signum. The gnathos in *Pionenta* does not have a quadrate dorso-caudal margin with two to four (occasionally five) widely separated, dorsally projecting teeth as found in *Tetracis* (Ferris & Schmidt, 2010). Once barcoding of the North America geometrid genera has been completed, the relationship of *Pionenta* can be established.

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Appendix: Annotated checklist of the taxa assigned to Antepione and Pionenta

Antepione Packard, 1876

imitata H. Edwards, 1884, New Mexico, Las Vegas [HT female, SEMC]
comstocki Sperry, 1939, syn. n., Arizona, Baboquivari Mts. [HT male, CNC]
constans (Hulst, 1898), syn. n., Arizona, Prescott [HT male, AMNH]
costinotata Taylor, 1906, Colorado, Durango [HT female, USNM] Note 1
indiscretata (H. Edwards), 1884, syn. n., New Mexico, Las Vegas [HT female, SEMC]

vanusaria (Strecker, 1899), syn. rev., New Mexico [HT male, FMNH]

thisoaria Guenée, 1857 [1858], fixed herein as eastern North America [HT female, MNHN]

- arcasaria (Walker, 1860), [HT female, BMNH]
- *azonax* (Druce, 1892) Guatemala, San Geronimo; Costa Rica, Volcan de Irazu [ST female, BMNH] Note 2

constricta (Warren, 1895), ? South America [HT male, BMNH] Note 2

depontanata (Grote, 1864), Maryland [HT male] Note 3

fuciferata (Packard, 1876), New York [HT male, MCZ]

rhomboidaria (Oberthür, 1912), Costa Rica, San Jose [STs, BMNH] Note 2

rivulata (Warren, 1897), Costa Rica [HT female, BMNH] Note 2

sulphuraria (Packard, 1873), New York, West Farms; Middle States [HT female, MCZ]

sulphurata (Packard, 1876) Note 4

tiselaaria (Dyar. 1912), Mexico, Minerale de Zacualpan [HT male, USNM]

Pionenta Ferris, 2010, gen. n.

ochreata (Hulst, 1898), comb. n., Arizona, Senator [HT male, AMNH] arizonata (Taylor, 1905), syn. rev., Arizona, Cochise Co., Huachuca Mts. [HT male, USNM]

dyari (Grossbeck, 1908), syn. rev., Arizona, Huachuca Mts. [HT male, USNM]

hewesata (Sperry, 1948), **syn. n.**, Arizona, Oak Creek Canyon, Todd's Lodge [HT female, AMNH]

ligata (Grossbeck, 1908), syn. rev., Arizona, Huachuca Mts. [HT male, USNM]

Notes:

- 1. Taylor stated in his original description that the HT was type number 9800 in the USNM. A recent attempt to locate the type failed, and it is presumed misplaced or lost. The TL was incorrectly stated as Prescott, Arizona in Parsons et al. (1999).
- 2. Barcoding of these taxa may ultimately indicate species distinct from thisoaria.
- 3. The type was originally placed in the collection of the Entomological Society of Philadelphia and subsequently in ANSP. In the 1960s, the bulk of the ANSP Lepidoptera collection went to CMNH. The type cannot be located in either ANSP or CMNH and is presumed lost.
- 4. Packard (1876) redescribed *Heterolocha sulphuraria* Packard, 1873 as *Antepione sulphurata*.