NEW OREAL PEDALIODINE BUTTERFLIES FROM ECUADOR AND COLOMBIA (NYMPHALIDAE: SATYRINAE: PRONOPHILINI)

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ABSTRACT
One new species and two new subspecies of Altopedaliodes Forster are described from southern Ecuador: A. halli n. sp., A. perita sorda n. ssp. and A. zsolti citra n. ssp. The species Altopedaliodes kruegeri Pyrcz is transferred to Pedaliodes and a new subspecies P. k. belmira n. ssp. is described from northern Colombian Central Cordillera. The, hitherto, unknown female of A. kurti Pyrcz & Viloria is described. The generic diagnosis of Altopedaliodes is discussed pointing out the insufficiency of solid proof for the monophyly of this taxon. Oreal Pronophilini of the northern Andes are briefly reviewed.

KEY WORDS: aedeagus, Altopedaliodes, Andes, new taxa, paramo, Punapedaliodes, Steromapedaliodes, Stipa, taxonomy

OREAL BIOME OF THE NORTHERN ANDES
The oreal biome of the northern Andes, roughly North of 7° South, is designated by the Spanish term - páramo. Many different, mainly non-forested plant communities can be found in paramo, however the most widespread are dominated by tussock grasses (SALGADO-LABOURIAU, 1980). Traditionally the paramo has been divided into three broad zones based on overall altitude and vegetation structure. From the highest elevation to the lowest, these three zones are called superparamo, grass paramo, and subparamo. The superparamo is a narrow zone of vegetation growing on rocky zones and coarse, sandy soil below the snowline at about 4000 – 5000 metres asl. This zone is characterised...
by having the lowest air temperature, precipitation, and by having the highest solar radiation
and night-frost frequency (VEILLON, 1989). The paramo is found at about 3200 metres
asl. (Exceptionally down to 2500 metres asl. due to local edaphic conditions (PYRCZ &
VILORIA, in press)) to 4400 metres asl. The vegetation of the grass paramo is composed
mainly of tussock or bunch-grasslands dominated by different species of Calamagrostis,
Stipa and Festuca Poaceae (PODBIELKOWSKI, 1987). This is the classical area of the
Bromeliaceae genus Puya and the Asteraceae genus Espeletia (frailejón) and its relatives.
The Espeletia group has seven genera (i.e. Carramboa, Coespeletia, Espeletia,
Espeletiopsis, Libanothamnus, Rulopezia, and Tamania) with ca. 80 species (SALGADO-
LABOURIAU, 1980). In undisturbed paramos the stem of Espeletia reaches a height of
several meters. They can be simple (unbranched) or branched (i.e., rosette trees). Within
the Espeletia group we can distinguish two major kinds of life forms: polycarpic (plants
that fruit more than once) and monocarpic (plants die after flowering and fruiting). There
is a trend for the caulirosulae species to grow in the paramo region whereas the arborescent
species tend to grow a lower elevation in the Andean forest belts or in the subparamo. The
lowest zone of the paramos, called subparamo, is also the most diverse. It is a shrub
dominated transition zone at 2800–3200 metres asl., exceptionally to 3500 metres asl.,
comprising elements from forest below and the grass paramo above. Occasionally, forest
communities (composed of Polylepis in the Rosaceae) are also found within the grass
paramo (SALGADO-LABOURIAU, 1980).

OREAL PRONOPHILINES IN THE NORTHERN ANDES

Oreal species can be defined as those, whose entire life cycle, from egg to imagine, is
linked with high altitude habitats above timberline. Oreal satyrines of the tribe Pronophilini
(as defined by MILLER, 1968) found in the Northern Andes – North of the Huancabamba
deflection in northern Peru - are very diverse, contrary to the opinion of some authors (i.e.
DESCIMON, 1986 and SHAPIRO, 1991), and represent at least ten genera. Three genera
- Paramo Adams & Bernard, Idioneurula Strand and Diaphanos Adams & Bernard (the
latter two considered by VILORIA (Ph.D.) as belonging to the tribe Erebiini) - can be
considered as strictly oreal (ADAMS & BERNARD, 1981; VILORIA, 1994). I. erebioides
(C. & R. Felder) occurring in the Colombian Eastern Cordillera, and D. huberi Adams &
Bernard, D. curvignathos Viloria and D. fuscus Viloria found in the Venezuelan Cordillera
de Mérida are associated exclusively with grassland paramos dominated by Calamagrostis
and Stipa Poaceae.

Other genera, such as Altopedaliodes Forster, Steromapedaliodes Forster (revised by
Dangond Adams & Bernard and Redonda Adams & Bernard are predominantly oreal nevertheless some of their representatives occur also in the subparamo and cloud forests below timberline (ADAMS & BERNARD, 1981). Three other genera, Pedaliodes Butler, Lymanopoda Westwood and Manerebia Staudinger are predominantly denizens of cloud forests with, however, numerous species adapted to the oreal biome (ADAMS, 1986). This particularly applies to Lymanopoda, a genus with approximately 10-15% species associated with paramo habitats (PYRCZ, Ph.D.). Oreal species of North Andean Lymanopoda are L. huilana Weymer, L. vivienteni (Apolinar), L. mirabilis (Staudinger), L. nevada Krüger and L. paramera Adams & Bernard. Several North Andean Pedaliodes sensu stricto are also strictly oreal, including P. palpita Adams, P. empsa (C. & R. Felder) and P. guicana Adams.

In some cases, the same species can adapt either to paramo or cloud forest depending on the locality. For example P. kruegeri is found in the Páramo Puracé (Colombia) in the open paramo densely covered with dwarf bamboo (PYRCZ, 1999), whereas in Papallacta (Ecuador) it flies in the forest gullies. A. perita, A. zsolti (PYRCZ & VILORIA, 1999) and A. nebris (ADAMS, 1986) occur alternately in the subparamo or in the lower paramo. The populations of L. samius (Westwood) in the Bogotá area (Cundinamarca) occur in the uppermost forest but the northern subspecies found in the El Tamá range is strictly associated with paramo grassland.

One genus, Punapedaliodes Forster comprising two species (P. flavopunctata Staudinger and P. albomaculata Weymer) is central Andean and occurs in the Bolivian and Peruvian puna grassland. One subspecies of the former species marginally penetrates into southernmost Ecuador.

**Acronyms for consulted collections**

- BMNH: The Natural History Museum, London, UK
- KWJH: Collection of Keith Willmott and Jason Hall, London, UK
- MB: Collection of Maurizio Bollino, Lecce, Italy
- MIIZ: Muzeum i Instytut Zoologii Polskiej Akademii Nauk, Warsaw, Poland
- MZUJ: Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland.
- PUCE: Museo de Entomología, Pontificia Universidad Católica del Ecuador, Quito
- PB: Collection of Pierre Boyer, Le Puy Sainte Réparade, France
- TWP: Collection of Tomasz Wilhelm Pyrcz, Warsaw, Poland

**DESCRIPTIONS OF NEW TAXA**
Altopedaliodes halli Pyrcz, n. sp. (Figs. 10, 13)

**DIAGNOSIS:** Recognised from the most similar *A. zsolti zsolti* by the darker, blackish brown upperside colour, and the absence of conspicuous HWV submarginal milky white dots.

**DESCRIPTION:** Male (Fig. 10): Head: eyes blackish, lustrous; labial palpi medium brown covered with chocolate brown hair; antennae to two fifth the length of costa, slender, dorsally dark brown, ventrally slightly lighter, club only slightly thicker than shaft, flattened. Thorax: dorsally and ventrally black, legs brown. Abdomen: dorsally black, ventrally grey brown. Wings: FW (length: 25mm, n=3) apex blunt, outer margin slightly concave. HW oval, outer margin without undulation. FWD uniform blackish brown; androconial patch covering median one fourth, entering discal cell, slightly extending along veins, the area along 1A separate; fringes brown with whitish scales in the interspaces visible from apex to vein M3. HWD uniform blackish brown. FWV greyish brown; a faint milky white postdiscal costal streak reaching into cell M2-M3; a row of five tiny, white submarginal dots; subapical, apical and marginal area from apex to vein Cu1 dusted with magenta and milky white scales, somewhat denser in subapical area. HWV dark brown, liberally speckled with magenta and milky white scales forming a ripple-like pattern; a short, faint costal milky white streak; a row of 5-6 tiny submarginal white dots parallel to outer margin.

**Male genitalia (Fig. 13):** Uncus straight and moderately long, gnathos well developed, half the length of uncus, saccus deep, valvae with smooth dorsal surface and without secondary process, aedeagus slightly contorted. Genitalia are very similar to *A. perita*.

**Female:** Hitherto unknown.

**TYPES:** Holotype (male): Ecuador, prov. Loja, Podocarpus National Park, Cerro Toledo, 3000m, IX.2003, I. Aldas leg., ex coll. MB, TWP. Paratypes (4 males): 3 males: same data as the holotype, MB; 1 male: Ecuador, Prov. Loja, Podocarpus National Park, Cajanuma, 2800m, 10.XI.1996, J. Hall & K. Willmott leg., KWJH.

**ETYMOLOGY:** This species is dedicated to Jason P. W. Hall, an English entomologist known for his numerous contributions to the knowledge of Ecuadorian Lepidoptera, particularly of the family Riodinidae, who discovered this new species alongside his colleague Keith Willmott.

**REMARKS:** This species is placed in the genus *Altopedaliodes* on the strength of its male genitalia agreeing with the generic diagnosis (VILORIA, Ph.D.), very similar to *Altopedaliodes perita*, and the underside colour pattern, also strongly reminiscent of other south Ecuadorian *Altopedaliodes*. Its wings are not as elongate as in other species of this genus found in southern Ecuador. *P. halli* occurs in the forest paramo ecotone in southern...
Ecuador. It is known so far exclusively from two localities, Cajanuma and Cerro Toledo, both situated in the Podocarpus National Park.

**Altopedaliodes perita sorda** Pyrcz, n. ssp. (Figs. 1, 2, 14)

*Pronophila perita* Hewitson, 1868: pl. 37, fig. 25
*Pedaliodes perita* (Hewitson); Butler, 1868: 170
*Altopedaliodes perita* (Hewitson); Forster, 1964: 148, 149, fig. 177 (genitalia); Pyrcz & Viloria, 1999: 121, fig. 4 (adult), 126, fig. 27 (male genitalia).

**DESCRIPTION:** Male (Fig. 1): Head, thorax and abdomen as in nominotypical (Fig. 3). Wings: FW length (25-27mm, mean: 25.8mm, n=7) larger than in nominotypical (23-25mm, mean: 24mm, n=14). FWD uniform blackish brown, darker than the chocolate brown of nominotypical and lacking four submarginal yellow dots. HWD uniform blackish brown. FWV surface blackish brown, darker than medium brown of nominotypical, four to five yellow dots, as on FWD, lacking the postdiscal faint irregular yellowish band apparent in nominotypical. HWV blackish brown, lighter and less patterned than nominotypical, with fainter triangular yellow postmedian and costal patches, and a more indented submarginal line than the regular, nearly parallel to outer margin one of nominotypical.

Male genitalia (Fig. 14): Valvae with a blunt tip, slightly shorter and wider than the nominotypical, otherwise similar.

**Female** (Fig. 2): Similar to the male but lighter patterned on FWD and HWD.


**ETYMOLOGY:** *sorda* – rubbish, trash. This subspecies is called after “el basurero”, literally rubbish heap, which refers to a litter deposit located in its type locality.

**REMARKS:** Even though Hewitson (1868) did not state the exact type locality of *Pronophila perita*, the original figure is very good and shows a series of characters clearly matching the individuals inhabiting the Eastern Cordillera along the border between the provinces of Morona-Santiago and Azuay. Nominotypical subspecies is also found in the Saraguro area. *A. perita sorda* is the southern subspecies occurs in the Podocarpus National Park and the Cordillera de Lagunillas along the border of the provinces of Loja and Zamora-
Chinchipe. It occurs in the lower paramo or in secondary grassland just below the timberline at 2800 metres asl. alongside Pedaliodes phoenicusa (Hewitson), Lymanopoda hazelana Brown and Manerebia ignilineata Dognin. In the Cordillera de Lagunillas along the Ecuador-Peru border it is found in the same habitat as its congener A. zsolti zsolti Pyrcz & Viloria.

Altopedaliodes zsolti citra Pyrcz, n. ssp. (Figs. 5, 15)

Altopedaliodes zsolti Pyrcz & Viloria, 1999: 120, figs. 5 (male), 26 (male genitalia)

DESCRIPTION: Male (Fig. 5): Head, thorax and abdomen as in nominotypical (Fig. 6). Wings: FW length: 23-24mm, mean: 23.4mm, n=5; fringes alternately milky white and brown. HW outer margin appears slightly undulate which is an effect of fringes’ milky white scales in the interspaces. FWD grey-brown, a shade darker than medium-brown of nominotypical; a row of four minute whitish subapical dots in R5-M1 to M3-Cu1 and a larger dot in Cu1-Cu2, not apparent in nominotypical. FWV postdiscal whitish band from costa to cell M2-M3 slightly better marked than in nominotypical. HWV patterned as in nominotypical but groundcolour darker brown; a well marked whitish costal patch reaching to vein M1 and another narrow one across cell M2-M3; the area between postmedian and submarginal lines suffused with light brown and whitish scales with a row of five white dots from Rs-M1 to Cu1-Cu2; submarginal line less indented than in nominotypical.

Male genitalia (Fig. 15): Subuncus rudimentary, short tip, compared to fully developed subuncus of nominotypical; valvae similar; saccus slightly shallower; aedeagus much shorter, barely half the length of nominotypical, the length of valvae.

Female: Hitherto unknown.


ETYMOLOGY: *citra* – lemon. This subspecies is called after of the locality of El Limón, near its type locality.

REMARKS: The nominate A. zsolti was described from the Podocarpus National Park, whereas A. zsolti citra occurs further North along the Morona-Santiago – Azuay border East of the locality of Gualaceo. It flies in the lower paramo at 3200-3400 metres asl. alongside much more common A. perita perita and A. flavopunctata nucea Pyrcz &
Viloria, the latter is being however more abundant at slightly higher elevations in the open *Stipa ichu* grassland.

*Pedaliodes kruegeri belmira* **Pyrcz & Rodríguez*** n. ssp., n. comb. (Figs. 7, 8, 16)

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*Pedaliodes paenoides* (Hewitson) var. *flavopunctata* Krüger, 1924: 28, name preoccupied by *P. albopunctata* var. *flavopunctata* Staudinger, 1894.

*Altopedaliodes flavopunctata* (Krüger); Adams, 1986: 247, figs. 1 (male genitalia) 22 (adult).

*Altopedaliodes kruegeri* Pyrcz, 1999: 225.

**DESCRIPTION:** Male (Fig. 7): Head, thorax and abdomen as in nominotypical subspecies (Fig. 9). Wings: FW (length: 22,5-23,5mm, mean: 23mm, n=5) smaller than nominotypical (length: 26,5-27,5mm, mean: 27mm, n=25). FWD and HWD uniform dark brown, lighter than blackish-brown of nominotypical. FWV and HWV similar to nominotypical but slightly lighter brown. HW submarginal yellow dots barely noticeable.

Male genitalia (Fig. 16): As illustrated.

Female (Fig. 8): FW (length: 22,5-23mm; mean: 22,8mm; n=5); fringes alternately white and dark brown. HW rounded; fringes brown. FWD and HWD greyish brown, lighter than in the male. FWV dull greyish brown; diffused white postdiscal costal streak; subapical and apical area dusted with whitish scales; a row of three submarginal white dots. HWV greyish brown; diffused white postdiscal band from costa to vein Cu2; anal area dusted with whitish scales; row of five submarginal white dots.

**TYPES:** Holotype (male): Colombia, Antioquia, Páramo de Belmira, 3000-3200m, 09.X.2002, G. Rodríguez leg., TWP. Allotype (female): Páramo de Belmira, Antioquia, 3200m, 16.IX.2001, 3200m, G. Rodríguez leg., GR. Paratypes (19 males and 4 females): 1 male, same locality and collector, 3200m, 16.IX.2001, GR; 15 males, same locality and collector, 3100m, 09.I.2002, 3100m, GR; 3 males: same locality and collector, 3000-3200m, 09.I.2002, TWP; 1 female, same locality and collector, 3100m, 09.I.2002, TWP; 3 females, same locality and collector, 09/01/02, 3100m, GR.

**ETYMOLOGY:** This subspecies is named after its type locality, the Páramo de Belmira.

**REMARKS:** This species is transferred herein to the genus *Pedaliodes*. Its wing shape (short forewing, rounded hindwing) and particularly male genitalia are typical of *Pedaliodes sensu stricto* and do not agree with the generic diagnosis of *Altopedaliodes* (Viloria, Ph.D.) by having a deep saccus, prominent dorsal process on the valva, and long, asymmetrical and contorted aedeagus.

This species was originally described by E. Krüger (1924) as *Pedaliodes paenoides*
var. flavopunctata, raised later to the specific rank and transferred to the genus Altopedaliodes by Adams (1986). Pyrcz (1999) pointed out that P. paeonidae var. flavopunctata is a junior homonym of Pedaliodes albopunctata var. flavopunctata Staudinger (1894) and he proposed a replacement name Altopedaliodes kruegeri. P. kruegeri kruegeri occurs in the Volcano Puracé massif in the Colombian Central Cordillera in Huila and Cauca. It was later discovered by this author in northern Ecuador, in the valley of Papallacta east of Quito. The population from Papallacta only marginally differs from the one found in the type locality, to an extent not justifying the identification of yet another subspecies. However, the population found in Antioquia is markedly different, which reflects most of all in much smaller size, lighter colour on both upper and underside and more uniform pattern of the HWV. The type locality, Páramo de Belmira is the highest elevation of the northern part of the Central Cordillera in the department of Antioquia, and the only one high enough to support paramo vegetation with typical ichu bunch grasses and Espeletia composites. It is well isolated by an area of lower mountains from larger units of paramo situated more than 100km further south in the Caldas department. It is therefore the only area in Antioquia to support an oreal fauna of butterflies.

The female of Altopedaliodes kurti Pyrcz & Viloria (Fig. 12)

Altopedaliodes kurti Pyrcz & Viloria, 1999: 119, figs. 1 (adult), 24 (genitalia).

DESCRIPTION: Sexual dimorphism little marked. The female FW (length: 21,5mm) same size as the male (Fig. 11). FWD and HWD uniform chestnut, glossy, lighter than the greyish brown of the male. FWV pattern similar but lighter, chestnut. HWV pattern similar, but lighter, with the milky white diffused postdiscal line running from M2 to Cu2, liberally dusted with delicate greyish pattern and a somewhat darker chestnut suffusion in the postdiscal area.

REMARKS: Altopedaliodes kurti was described based on a single male specimen collected by the British Ornithologist Expedition “Parrots in Peril” on the Cerro Toledo above Yangana in the Podocarpus National Park. Later, this species was also found some 50kms southwards in the Cordillera de Lagunillas. Several males were collected perfectly matching the descriptive type, thus confirming the validity of this species. It appears that A. kurti occurs in open paramo grassland from 3200 metres asl. up, being more common on windy, westerly slopes at 3400-3600 metres asl. It occurs alongside Lymanopoda ichu Pyrcz, Willmott & Hall and an undescribed subspecies of Punapedaliodes flavopunctata (Staudinger).

DISCUSSION
FORSTER (1964) described as many as 43 new genera of Neotropical Satyrinae. He divided, among others, the most speciose worldwide genus of this subfamily, Pedaliodes BUTLER (1867), into 13 smaller entities based primarily on the structure of male genitalia, with an emphasis on the shape of the aedeagus. Some authors, including HAYWARD (1967), DE VRIES (1987) and D’ABRERA (1988), completely disregarded his ambitious attempt to reorganise the systematics of this complex group of Andean butterflies. Others, ADAMS & BERNARD (1977, 1979 and 1981) and ADAMS (1986), tried to cope with the “forsterian revolution”. They revised and retained the validity of several genera introduced by FORSTER, synonymised others, and even raised new pedaliodine genera of their own (Paramo, Dangond and Redonda). PYRCZ (1999) and PYRCZ & VILORIA (1999) concurred with the modifications made by their predecessors but did not discuss in details the generic taxonomy of the Pedaliodes complex. VILORIA (Ph.D.) carried out a cladistic analysis of this section of the tribe Pronophilini and demonstrated the monophyly of Pedaliodes sensu lato. He also confirmed the monophyly of some of the forsterian genera, pointing out however that simple diagnostic characters of others could well be homoplasies (VILORIA, op. cit.). Particularly, the genus Pedaliodes sensu FORSTER (1964) appeared an assemblage of all the species that do not present any highly distinctive characters of the aedeagus but not necessarily monophyletic.

According to VILORIA (op. cit.) the adults of Altopedaliodes can be recognised by small to medium size, no marked sexual dimorphism, antennal club formed gradually, narrow forewings, wing margins rounded and smooth, rounded apex, and androconial patches present on forewing upperside. Male genitalia of Altopedaliodes are characterised by small saccus, moderately long aedeagus, straight or slightly curved dorsoventrally, only slightly laterally asymmetrical, never contorted, sub-rectangular valvae, dorsally slightly serrate, with rudimentary or absent ampullar process in subapical position. The characters that according to VILORIA (op. cit.) define Altopedaliodes prove mostly quantitative and some are inconsistent. Small androconial patch on male forewing upperside is a putative apomorphy of Altopedaliodes. However, specialised androconial scales however lack in Altopedaliodes kurti PYRCZ & VILORIA (1999). The aedeagus of A. zsolti is long and arched as in some Panyapedaliodes and Parapedaliodes sensu FORSTER (1964). On the other hand in some Panyapedaliodes it is nearly as short and straight in as in Altopedaliodes. Valvae with a serrate dorsum and rudimentary process on the ampulla are present in Altopedaliodes, Panyapedaliodes as well as in many Pedaliodes sensu stricto. Elongate wings and small size of Altopedaliodes are certainly convergent adaptations to high elevation habitats characterised by harsh climate as in other oreal pronophilines.
(Lymanopoda and Manerebia). PYRCZ (in prep.) has recently discovered in northern Peru a small forest-paramo ecotone species externally similar to Altopedaliodes, whose genitalia are characterised by the absence of subuncus, the primary character defining north Andean oreal genera Paramo and Redonda. The cladograms constructed by VILORIA (op. cit.) base exclusively on adult male morphology, with heavy bias on simple genitalic structures, whose interpretation from the phyletical point of view is difficult and can be highly subjective. A thorough revision of Altopedaliodes is required with the use of far more characters, including early stages morphology and chaetotaxy, female genitalic morphology and molecular data. Until then, despite the expressed above doubts, I retain the validity of the genus Altopedaliodes and follow the systematic arrangement as proposed by VILORIA (op. cit.).

Altopedaliodes included originally five species: A. tena (Hewitson), A. reissi (Weymer), A. perita (Hewitson), A. nebris (Thieme) and A. pasicles (Hewitson), the latter actually a subspecies of A. tena. PYRCZ & VILORIA (1999) described further species: Altopedaliodes zsolti and Altopedaliodes kurti. The complete catalogue of Altopedaliodes comprises also A. kruegeri PYRCZ (1999), the described herein A. halli, as well as A. cocytia (C. & R. Felder), considered by ADAMS (1986) as Punapedaliodes, transferred by PYRCZ & VILORIA (in press) to Altopedaliodes and another related species restricted to the El Tamá range on the Venezuela - Colombia border (PYRCZ & VILORIA, in press).

The genus Punapedaliodes FORSTER (1964) was synonymised with Altopedaliodes by LAMAS [1997]. However, VILORIA (Ph.D.) disagreed pointing out its very distinctive genitalia, especially the low-domed, almost flat tegumen, deep saccus longer than tegumen, and especially the asymmetrical and slightly contorted, laterally compressed at base, large and broad aedeagus membranous at distal extremity, with apical aggregation of multiple tiny spines. Punapedaliodes is characterised by the lack of FWD specialised androconial scales but this is not an exclusive feature, also shared by Altopedaliodes kurti.

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REFERENCES


Plate 1. Adults (dorsum/venter)
Fig. 1 Altopedaliodes perita sorda holotype male
Fig. 2 Altopedaliodes perita sorda allotype female
Fig. 3 Altopedaliodes perita perita male
Fig. 4 Altopedaliodes perita perita female
Fig. 5 Altopedaliodes zsolti citra holotype male
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Fig. 7 Pedaliodes kruegeri belmira paratype male
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Fig. 13. *Altopedaliodes halli* male genitalia

Fig. 14. *Altopedaliodes perita sorda* male genitalia

Fig. 15. *Altopedaliodes zsolti citra*

Fig. 16. *Pedaliodes kruegeri belmira* male genitalia