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# Defining generic limits in Syndesini MacLeay, 1819 (Coleoptera: Lucanidae: Syndesinae) through taxonomy and geometric morphometrics

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ABSTRACT

A comparative taxonomic study was performed between the Syndesini genera *Syndesus* MacLeay, 1819 and *Psilodon* Perty, 1830. Both taxa are redescribed, with the addition of more precise diagnostic traits, including the description of male and female genitalia. We provide comparative remarks to support the separation of both genera, with additional information obtained through the application of geometric morphometric analysis to the following morphological structures: right mandible of males (RMM); lateral view of left mandible of males (LMM); lateral view of males pronotal tubercle (PT); dorsal face of male and female pronotum (DFP); dorsal face of male and female elytra (DFE). The shapes of all analysed traits showed to be different through the performance of Principal Component Analyses producing two well-define clusters, except for the elytral shape which showed a high superposition, however all Procrustes and Mahalanobis distances showed significant differences, supporting the existence of two Syndesini genera instead of one. It was also possible to register a significant influence regarding the biogeographic distribution of the specimens, obtaining statistical differences when comparing the shape data from the Australasian and Neotropical biogeographic dominions, suggesting a strong relation between *Syndesus* and *Psilodon* divergence and the Gondwanan vicariant events. Finally, a checklist was provided including all the described species for both genera.

## 1. Introduction

Stag beetles from Syndesinae MacLeay, 1819 (Coleoptera: Lucanidae) represent one of the less diversified subfamilies in Lucanidae (Holloway 2007). Historically Syndesinae has been composed of three or four genera depending on the author, with around 30 described species. The first two genera are *Sinodendron* Hellwig, 1792 and *Ceruchus* MacLeay, 1819 which are restricted to the Holarctic region (Howden & Lawrence 1974), the third, *Syndesus* MacLeay, 1819 is distributed in Australia, New Caledonia and New Zealand, with some authors extending its distribution to South America, and the last one, *Psilodon* Perty, 1830, distributed along South America and considered by several authors as a synonym of *Syndesus* due to the high resemblance shared by both taxa.

While *Sinodendron* and *Ceruchus* have had a stable classification at the generic level, *Syndesus* and *Psilodon* lack a consensus. *Syndesus* was described as the type genus of Syndesidae, now recognized at the subfamily level. According to MacLeay (1819) description of *Syndesus cornutus* (Fabricius, 1801) (type species), male specimens present an elongate and cylindrical body, with convex shape; small and transverse head; labrum hardly distinct; mandibles almost straight; antennae glabrous with seven lamellae; tibiae serrate. Females are close to males except for the mandibular shape. MacLeay described *S. cornutus* based on *Sinodendron cornutum* Fabricius, 1801, both apparently from Tasmania but it is not clear if both authors had access to the same material as *S. cornutum* was described with antennal club six-lamellate and *S. cornutus* with seven lamellae.

*Psilodon* Perty, 1830 was described for Brazil based on a female collected by K.F.P. von Martius and J.B. von Spix during their expedition in Brazil (1817–1820) (Papavero 1971). *Psilodon schuberti* Perty, 1830 was the first described species, defined as being close to *Sinodendron*

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with the following characteristics: body dark with brownish tones at antennae; head rugose and somewhat excavate at frons; pronotum punctate with well-defined discal groove; scutellar shield smooth; elytra carinate; mandibles with erect setae; tibiae serrate and enlarged apically. The epithet proposed by Perty was probably based on the lack of well-define teeth of the specimen. Perty never mention the number of antennal lamellae.

Two years later Gray (1832) described a new genus from Brazil with the type species *Hexaphyllum brasiliensis*, in this case, based on a male collected in the state of Rio de Janeiro, and despite the high resemblance between Perty's and Gray's specimens, there were only considered as belonging to the same species by van Roon (1910). The epithet proposed by Gray was based on the presence of six lamellae at the antennal club. After this work, posterior authors continue to use *Hexaphyllum* as the valid genus, based on the number of lamellae (Hope 1840; Buquet 1840; van Roon 1910; Didier 1929; Luederwaldt 1935).

Didier and Séguy (1953) in their catalogue, and other authors such as Holloway (1968; 1997), Howden & Lawrence (1974), and Ratcliffe (2002) continued recognizing *Psilodon* as a valid genus, being the only South American representative of Syndesini MacLeay, 1819. In Benesh (1960), *Psilodon* and *Hexaphyllum* are considered for the first time synonyms of *Syndesus*, as he probably agreed with the observations made by Burmeister (1847a) and Arrow (1938) who stated that, given the high morphological resemblance between *Syndesus* and *Hexaphyllum* (=*Psilodon*), considering them as different taxa would represent an unnatural separation, they also argued that the number of antennal lamellae, six for *Hexaphyllum* and seven for *Syndesus* was not enough to establish a division between the South American specimens and the Australasian ones.

After Benesh's work in 1960, different authors such as Maes 1992; Krajcik 2001; Krajcik 2003; Holloway 2007; Onore et al., 2011, continued recognizing *Syndesus* as the only valid taxon, however, new species for *Psilodon* continued to be described (Martínez & Reyes-Castillo 1985; Boucher 1993; Pardo-Locarno & Ríos-Málaver 2011; Grossi & Aguiar 2014) and some authors, as Holloway (1968; 1997), Howden & Lawrence (1974), and Ratcliffe (2002) maintained the use of both genera as independent taxa.

There is no doubt that both genera are strongly related, they are even difficult to separate by non-specialists, but considering them as a unique taxon would be obscuring the disjunct distribution and morphological differences among both taxa (Woodruff 2009). In addition the lack of genetic studies, taxonomic revisions for both genera, the difficulty to accessing type material for most species, and the low representation of these specimens in most world entomological collections hinder the possibility of establishing the generic limits between *Psilodon* and *Syndesus*.

The lack of a taxonomic consensus for these genera represents a limitation for the definition of the Syndesini tribe and the development of evolutionary studies at a suprageneric level. In order to reduce these inconsistencies, we conducted a taxonomic study on *Syndesus* and *Psilodon* specimens which were deposited in different entomological collections, providing a species checklist for both genera, a redescription, and the definition of new diagnostic traits. Additionally, with the aim of reducing the subjectivity which traditional taxonomic descriptions are subjected to, we propose the use of geometric morphometric techniques as a support to the morphological descriptions and a validation for the diagnosis. With these techniques it is possible to study the shape variation of different structures, allowing the visualization of slight and strong morphological changes, and the application of statistical analyses (Klingenberg 2013).

## 2. Materials and methods

### 2.1. Specimens and taxonomic material

A total of 107 specimens from all species of *Psilodon* and *Syndesus* were examined. Specimen of *Syndesus macleayi* Boileau, 1905 and *Syndesus punctatus* Boileau, 1905 were studied using high quality photographs of Holotypes deposited in the Muséum national d'Histoire naturelle of Paris, which were gently offered by Mr Christophe Rivier and Antoine Mantilleri. Dry collection material is deposited in the following collections.

**AMBC** Ayr Bello collection, included at the CEMT (Coleção Zoológica da Universidade Federal de Mato Grosso. Brazil, Mato Grosso, Cuiabá).

**CEMT** Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso. Brazil, Mato Grosso, Cuiabá.

**CERPE** Coleção Entomológica da Universidade Federal Rural de Pernambuco. Brazil, Pernambuco, Recife.

**CZPB** Coleção Zoológica Paulo Buhrnheim, UFAM, Brazil, Amazonas, Manaus.

**EPGC** Everardo and Paschoal Grossi Collection. Brazil, Rio de Janeiro, Nova Friburgo.

**HEC** Hope Entomological Collections, Oxford University Museum of Natural History. UK, Oxford.

**MNHN** Muséum national d'Histoire naturelle. France, Paris.

**MNRJ** Museu Nacional Rio de Janeiro. Brazil, Rio de Janeiro.

**MZUEFS** Museu de Zoologia Universidade Estadual de Feira de Santana. Brazil, Bahia, Feira de Santana.

**NZAC** New Zealand Arthropod Collection. New Zealand, Auckland.

**UMSP** University of Minnesota – Saint Paul Insect Collection. United States, Minnesota, St. Paul.

**ZIN** Zoological Institute of Russian Academy of Sciences. Russia, St. Petersburg.

### 2.2. Morphological characters

Descriptions for both genera are based on the following conventions. Specimens were studied using a dissecting microscope Zeiss Stemi 508 at 0.63 to 0.50x under fibber optic illumination. ***Size*** was determined using a 0–150 mm digital calliper. ***Length*** was measured from the apex of the mandible to the apex of elytra. ***Width*** was measured at the widest point of the body, mainly across the pronotum and the elytral humeri. ***Colour*** as determined under LED spot illumination. The characteristics of the body surface such as the presence of punctures or setae were based on the described macroscopic types by Holloway (1997; 2007) and. ***Vestiture*** appearance is based on description made under light magnification. ***Puncture size*** and ***density*** are defined according to Paulsen (2005). ***Discrimen***, is defined as a discrete longitudinal groove present along metaventrite concavity, nevertheless, this trait is not present as a complete suture in most specimens, instead is possible to see a superficial groove or a glabrous longitudinal region. All male and female ***Genitalic*** structures are named according to Holloway (1960, 1961, 1998 and 2007), Lawrence et al. (2011), and Cristóvão & Vaz-de-Mello (2021) consisting on the 9th and 10th abdominal segment, referred as the terminalia. Descriptions of male genitalia were made considering the ventral, dorsal and lateral views including characteristics based on the basal piece, parameres, median lobe and internal sac. For the females there was included information related to a portion of the sclerotized structures on the 9th and 10th abdominal segments, and reproductive structures *per se*, only considering the ventral view. Dissections of male and female genitalia were conducted as proposed by Grossi & Aguiar 2014.

### 2.3. Geometric morphometric analysis

As a complement for the taxonomic descriptions, geometric morphometrics tools were performed using 81 specimens of *Psilodon* Perty, which were photographed, and represents all the described species according to the *sensu* proposed in Grossi & Aguiar (2014) (n = 51), and several undetermined specimens from Brazil, Venezuela and Trinidad and Tobago (n = 31). In the case of *Syndesus* MacLeay, a total of 25 images were used. And additional image of the fossil species *Syndesus*

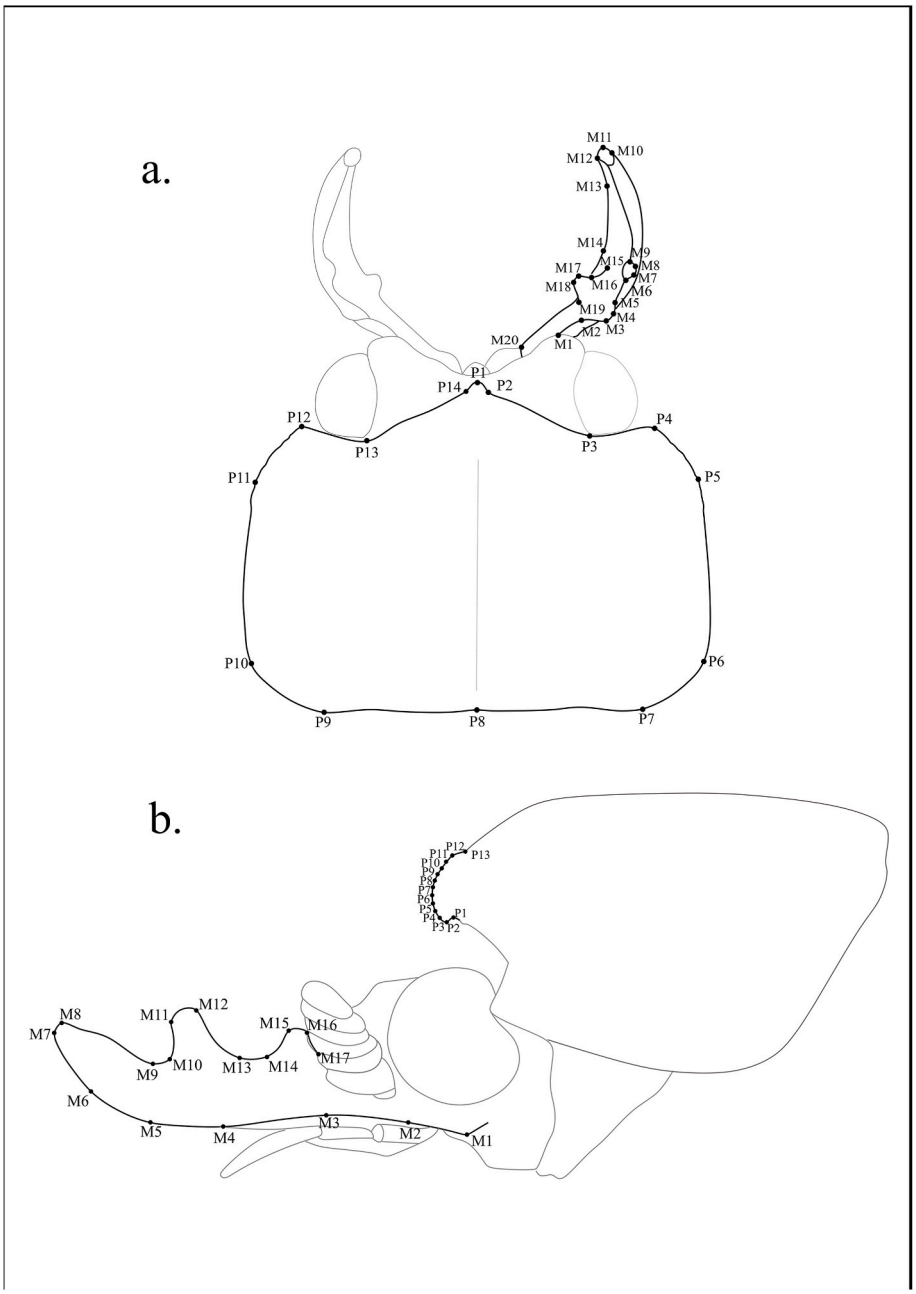


**Fig. 1.** Proposed landmarks for **a)** RMM (M1-M20) and DFP (P1–P14). **b)** LMM (M1-M17) and PT (P1–P13).

*ambericus* Woodruff, 2009 was added to analyse the lateral view shapes of some structures.

All photographs were taken using a digital camera coupled to a DIGILAB DI-150B stereoscopic microscope. Each image was posteriorly edited when needed, using GIMP v.2.10.30.

In order to capture the male and female shape of specimens from both genera, a series of landmarks were defined, standardized and digitalized using the curves tool with equidistant points of TPSdig2 v.2.30 (Rohlf 2017). The analysed traits were the **right mandible of males (RMM)** with 20 landmarks (Fig. 1a. M1-M20); lateral view of **left mandible of males (LMM)** with 17 landmarks (Fig. 1b. M1-M17); lateral view of **pronotal tubercle (PT)** with 13 landmarks (Fig. 1b. P1–P13); dorsal face **of male and female pronotum (DFP)** using 14 landmarks (Fig. 1a. P1–P14); dorsal face of **male and female elytra (DFE)**, with 24 landmarks (Fig. 2a. E1-E24).

Each analysis was performed separately. In several cases, it was not possible to use the total number of images obtained, as the original position or photographs of some specimens coming from historical collections hindered the standardization and definition of all landmarks, furthermore, given the origin and importance of some specimens, we tried to avoid excessive manipulation. Thus the number of images used for dorsal surface of pronotum and elytra were higher than the used for mandibles and lateral view images (see Table 1).

Before conducting the morphometric analysis, all traits were digitized twice in order to test every landmark against definition error through the performance of a Procrustes ANOVA using MorphoJ v.1.07a (Klingenberg 2011), comparing the values of the mean squares of the error component of variation and individuals.

Using the software MorphoJ v.1.07a, a Procrustes Superposition analysis was performed to all analysed specimens, in order to remove the influence of size, position and orientation to shape variables (Rohlf & Slice 1990). With these variables a covariance matrix of the individual shape was performed in order to proceed with all corresponding multivariate analysis.

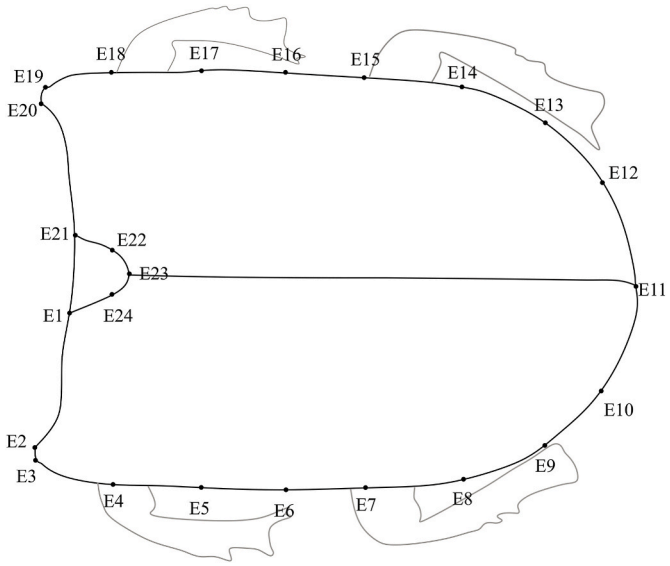


**Fig. 2.** Proposed landmarks for DFE (E1-E24).

**Table 1**
List of images used for geometric morphometric analyses of each structure.

| Structure | Number of analysed images |
|---|---|
| RMM | *Psilodon* (32)/*Syndesus* (19). **51** |
| LMM | *Psilodon* (27)/*Syndesus* (15). **42** |
| PT | *Psilodon* (27)/*Syndesus* (15). **42** |
| DFP | *Psilodon* (57)/*Syndesus* (25). **82** |
| DFE | *Psilodon* (57)/*Syndesus* (25). **82** |

To graphically visualize the shape space, a Principal Component Analysis (PCA) was performed for all the digitalized traits covariance matrices independently (Pearson 1901). Additionally, a Canonical Variate Analysis (CVA) was performed as a discriminant analysis using the classifiers **Genus** and **Biogeographic dominion**. A permutation test (10 000 runs) between groups was used to calculate the statistical relationship between groups using Mahalanobis and Procrustes distances showing the respective *p* values. All PCA and CVA figures obtained in MorphoJ were posteriorly edited using the software Inkscape 1.1.2 (b8e25be833, 2022-02-05).

## 3. Results

### 3.1. Taxonomic results

#### 3.1.1. Checklist of Syndesini MacLeay, 1819 genera and species

*Syndesus* MacLeay, 1819.
Fig. 3 a-f.
*S. cornutus* (Fabricius, 1801) (*Sinodendron*) – **Australia and New Zealand**.
= *Lucanus parvus* Donovan, 1805.
*Syndesus cancellatus* (Montrouzier, 1860) (*Rhyssonotus*) – **New Caledonia**.
*S. macleayi* Boileau, 1905 - **Australia**.
*S. punctatus* Boileau, 1905 - **New Caledonia**.
*Psilodon* Perty, 1830.
= *Hexaphyllum* Gray, 1832.
= *Syndesus* MacLeay, 1819 (partim).
Fig. 4 a-l.
*P. schuberti* Perty, 1830 - **Brazil**.
= *H. brasiliensis* Gray, 1832.
*Psilodon westwoodi* (Hope, 1840) (*Hexaphyllum*) - **Colombia**.
= *Hexaphyllum aequinoctiale* Buquet, 1840.
*Psilodon seguyi* (Didier 1929) (*Hexaphyllum*)- **Ecuador**.
*Psilodon xerophilicum* Martínez & Reyes-Castillo, 1985 - **Brazil**.
*Psilodon gilberti* Boucher, 1993 - **Bolivia**.
*Psilodon paschoali* Pardo-Locarno & Ríos-Málaver, 2011 - **Colombia**.
*Psilodon luki* (Onore et al., 2011) (*Syndesus*) - **Ecuador**.
*Psilodon buhrnheimi* Grossi & Aguiar 2014 **– Brazil**.

#### 3.1.2. Taxonomic diagnosis and descriptions

*3.1.2.1. Syndesus MacLeay, 1819.* **Examined material: *S. cornutus*: AUSTRALIA**, VIC Mitcham/Melbourne, 27.ii.1994, at light, Leg.G.J. Krake 1♂ (CERPE); same data except: 14.i.1995 1♂ 1♀ (CERPE); Acacia Plateau, 2.i.1994 – N.NSW, De Keyzer Leg. 1♂ 1♀ (CERPE); "Automontage Image FNZ/61 2007/**NEW ZEALAND**: Holloway/Infesting Oak door, Post Kings College, Chapel, Otahuhu, 29.i.1968. 1♂ (NZAC); Private Beg 92 170, Auckland, NZAC04193716/Illustrated, D. W. Helmore, 5.ii.90/In cop, 30.iv.1982/AK, Papatoetoe, iv.1982, F.J. Muller, in old Eucalyptus logs. 1♂ (NZAC); Auckland, NZAC04195439/AK, Whenuapai, 5.iii.1989, M. Manning/Attracted to light inside house at night. 1♂ (NZAC); Auckland, NZAC04195823/caught in light trap, m research sta./AK, Pakekche, 27.ii.1992, TJB Herman. 1♂ (NZAC); *S. cornutus*, (Fabricius, 1801), ♂, det. S.E. Thorpe 2003/Auckland, New Zealand, NZAC04191849/AK, Glen Innes, Tahuna Torea Res, on wing in evening, 4.iii.2003, Se Thorpe. 1♂ (NZAC); AK, Glen Innes, Tahuna Torea Res, ex rotten tree slump, 4.iii.2003, SE Thorpe/*S. cornutus*, (Fabricius, 1801), ♀, det. S.E. Thorpe 2003. 1♀ (NZAC); WO between Eureka and Newsteak iii.1970, Mr. Appelton./In building lavatory. 1♂ (NZAC)/NZAC04193118/Adult em 27.ii.1991, Reared: B.A. Holloway/AK, Birkenhead Larva: 22.x.1990, D. Longworth./Larva in old post, Chelsea, Sugar refinery. 1♂ (NZAC); same data except: Adult em. 24.ii.1991. Larva: 23.x.1990. 1♂ (NZAC); NZAC04192479/*S. cornutus* (Fabricius, 1801) Holloway 2007/Ex. Rotting, Floor Boards, Permrose, Auckland, 26.iii.1969, Termite Insp. 1♀ (NZAC); same data: 2♂ (NZAC). **Holotype male of *S. punctatus*** (Examined by photographs by Antoine Mantilleri – 2013 and Christophe Rivier - 2022) labelled: a) old white handwritten label, cancellatus, "not possible to read"; b) Ex coll Armitage; c) Type, H.B.; d) Muséum Paris, 1937, coll. R. Didier (ex. Coll. H. Boileau).; e) TYPE; f) Holotype, *S. punctatus* Boileau, 1905; g) Holotype; h) MNHN, EC3911. **Holotype male of *S. macleayi*** (Examined by photographs by Christophe Rivier - 2022) label: a) Victoria; b) Type H.B.; c) TYPE; d) Muséum Paris; e) Holotype; f) HOLOTYPE, *S. macleayi* Boileau, 1905; g) MNHN, Paris, EC14288; ***S. cancellatus*** labelled: MNHN, no further data 1♂ (MNHN); a) Ex: Musaeo GAMBEY 1892; b) Muséum Paris, 1952, Coll. R. Oberthur. 1♀(MNHN).

**Diagnosis:** specimens with strong sexual dimorphism at mandibles, labrum, antennae and pronotum. Males and females with sub-cylindrical (Australian species) to somewhat robust body (New Caledonian species). Head anteriorly emarginate, with strongly punctate surface. Supra-antennal projection with conspicuous carinae. Antennae with six to seven lamellae. Male mandible with one external strong tooth located medially, internal face with a laminar tooth, in New Caledonian species extended form base to apex, for Australian species ending before apex, producing in some specimens a reduce tooth-like projection; females mandibles curved upwards, with almost acuminate apex, also with a somewhat laminar tooth extended form base to apex along dorsal face, stronger at base. Gula conspicuous, convex, visible on lateral view. Labrum with concave and almost smooth surface, sometimes with a strong excavation, apex truncate or bilobed. Shape of pronotum convex; antero-lateral angles rounded to somewhat oblique; discal groove strong and complete, sometimes more superficial in females; pronotal tubercle conspicuous, in males, extended anteriorly covering median portion of head, sometimes extended beyond labrum, reduced in females and strongly transverse. Elytral striate, with strong punctation, also with interstrial costae, varying in number depending on the species. Ventrally

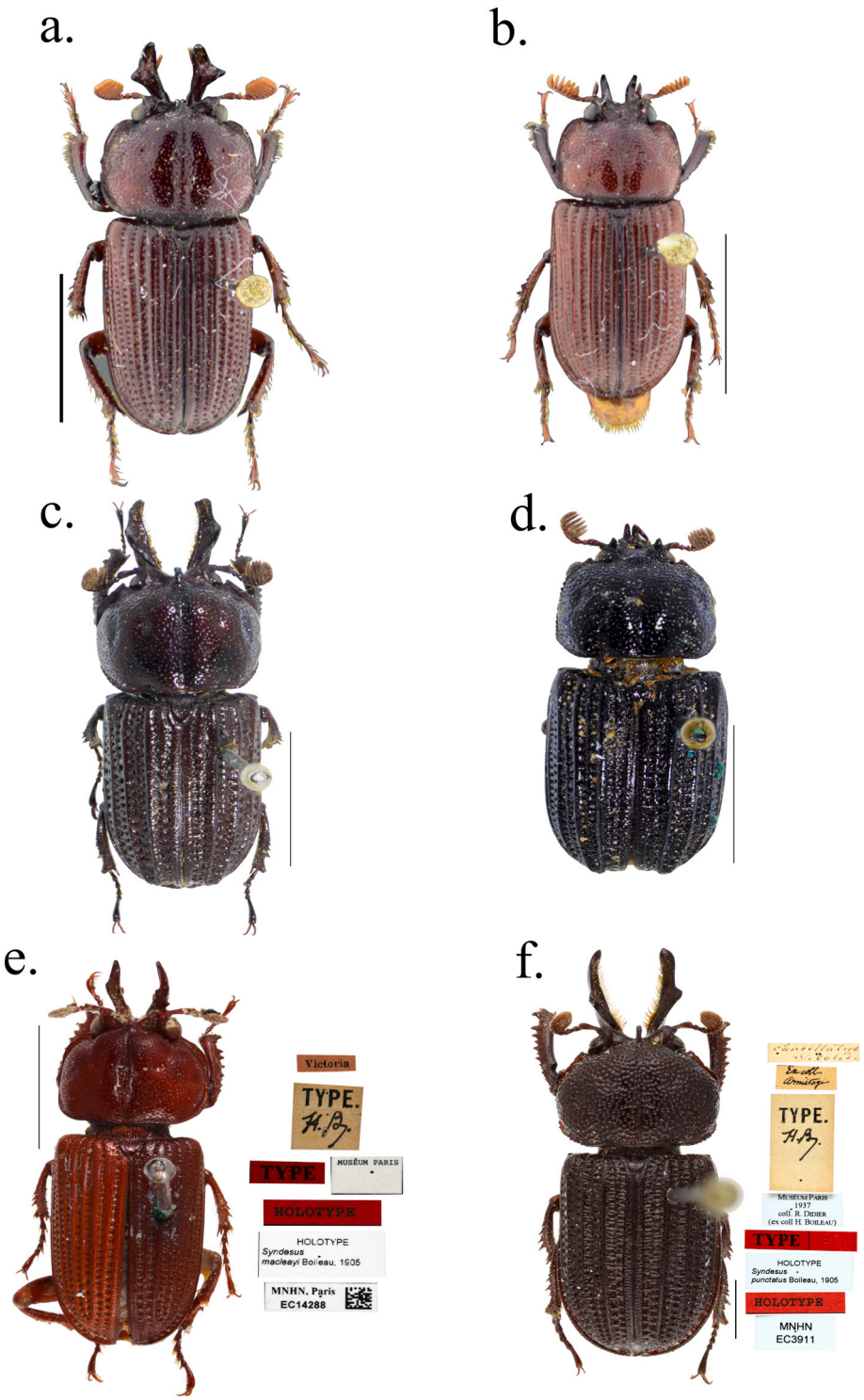


**Fig. 3.** Dorsal habitus of *Syndesus* MacLeay, 1819 species. **a)** *S. cornutus* Males. **b)** *S. cornutus* Female. **c)** *S. cancellatus* Male. **d)** *S. cancellatus* Female. **e)** Holotype male. MNHN *S. macleayi* (Photo by C. Rivier 2022). **f)** Holotype male. MNHN *S. punctatus* (Photo by A. Mantilleri 2013).

with a narrow and inconspicuous prosternal process; meso and metaventrite convex; discrimen present as a shallow groove, mainly visible posteriorly. Abdominal ventrites with fine and contiguous punctuation, also with a transverse carina extended through posterior margin of every ventrite. Male aedeagi symmetric, narrowed anteriorly; median lobe enlarged basally; dorsal cross bar "V" to somewhat "U" shaped, sometimes forming a subtriangular median structure. Female genitalia with elongate styli and gonocoxites abruptly narrowed anteriorly.

**Description Male:** ***Size*****:** *Total length*: 6.85–16.01 mm. *Total width*: 2.79–6.52 mm. ***Colour*****:** Most specimens with light brown tones to dark-red, sometimes somewhat black. ***Head*****:** Transverse, anteriorly strongly emarginate, partially concealed by ponotum; surface strongly punctate, some species with a partially smooth area at anterior portion of head; punctures dense and coarse with inconspicuous to somewhat conspicuous strongly curved setae; anterior edge with smooth to shagreened surface; labrum projected between mandibles, smooth, rounded to truncate at apex. Mentum subtrapezoidal, with two lobes at anterior edge, producing an emargination, also with large to somewhat coarse

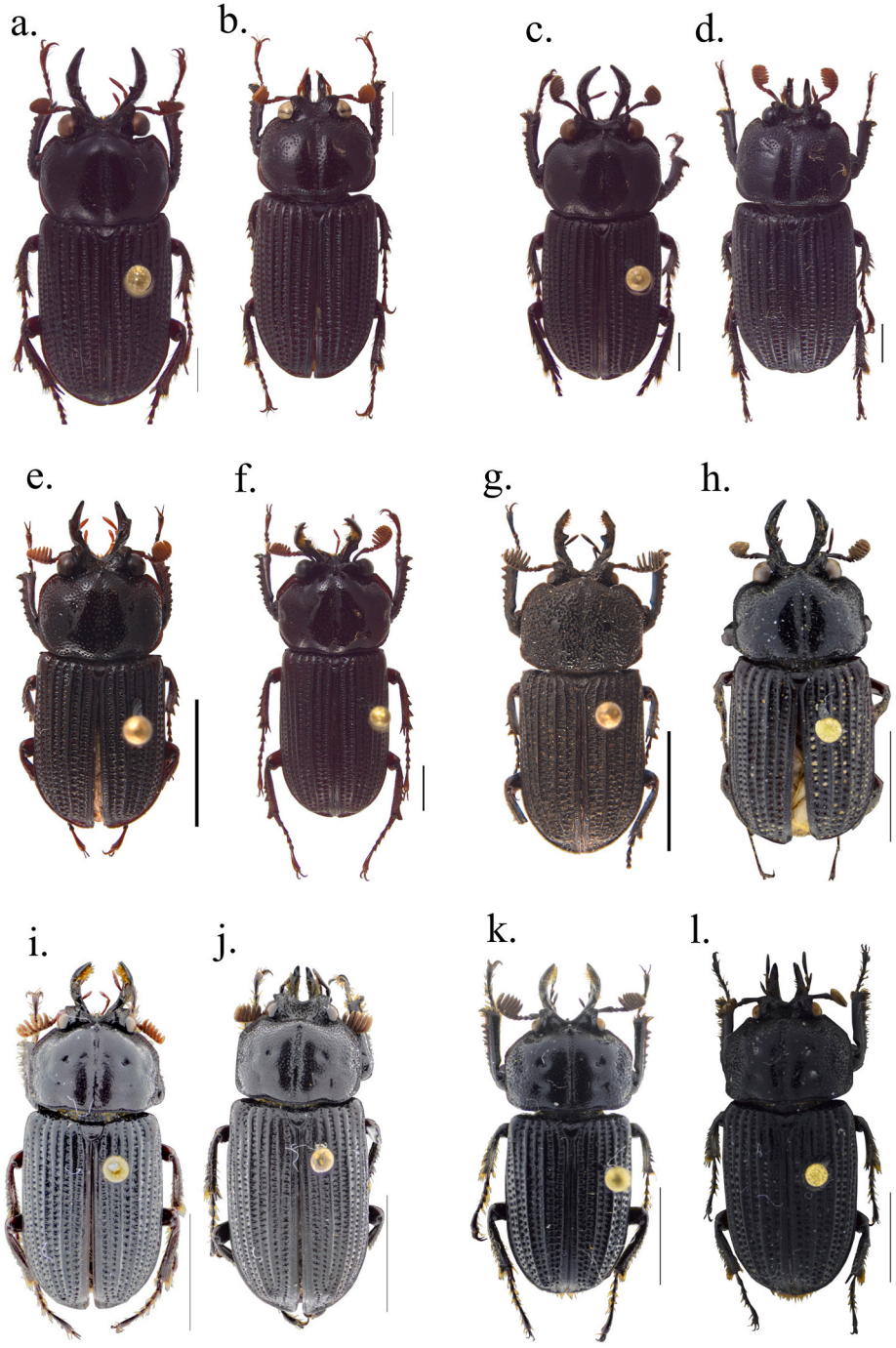


**Fig. 4.** Dorsal habitus of *Psilodon* Perty, 1830 species. **a)** *P. schuberti* Male. **b)** *P. schuberti* Female. **c)** *P. xerophilicum* Male. **d)** *P. xerophilicum* Female. **e)** *P. buhrnheimi* Male. **f)** *P. gilberti* Male. **g)** *P. wetwoodii* Male. **h)** *P. paschoali* Male. i) *P. seguyi* Male. **f)** *P. seguyi* Female. **g)** *P. luki* Male. **h)** *P. luki* Female.

punctures. Gula conspicuous, sub-trapezoidal, from strongly transverse to elongate, with an almost entirely carinate surface, carina smooth, anterior portion with contiguous large to coarse punctures and appressed to strongly curved setae. Gena with dense to moderate coarse punctuation and long appressed setae. Mandibles symmetric with one external tooth, and one internally, internal tooth laminar, complete or almost from base to apex; internal and external face with dense, large to coarse punctuation, internal and external face with suberect to curved setae, some species with a continuous line of conspicuous setae from base to apex of internal portion; apex acute to truncate. Supra-antennal projection present, strongly carinate in some species, when carinae reduced apex of projections truncate. Antennae with six to seven lamellae. ***Pronotum*:** Shape convex, sometimes with lateral constrictions, anterior margin projected anteriorly, with a narrow and conspicuous tubercle, distinctly extended anteriorly, reaching anterior margin of head; anterior angles reaching posterior margins of eyes; discal groove present, from complete and strong to superficial or absent; surface with moderate to coarse punctuation, dense to contiguous; lateral pronotal carina present, separating disc from hypomeron, almost complete and continuous with posterior and anterior margins, only interrupted at median portion of anterior margin, with scalloped surface and minute simple setae. ***Elytra*:** Elytral humeri not striate, with tooth-like projections; surface with several striae, each with coarse punctures and minute barbed setae; also with interstrial costae ending at an apical interstrial joint. Epipleuron complete to apex, distinctly visible in lateral view, with a concave surface, and contiguous to dense punctuation,

moderate to somewhat coarse. ***Legs*:** Tibiae serrate. Protibiae with strong teeth from base to apex and suberect to decumbent setae. Meso and metatibiae with similar appearance, serrate, with several teeth increasing in size distally, more acute than protibial ones, with suberect setae; apex enlarged with variable number of tooth-like projections. ***Venter*:** Prosternal anterior and posterior margins carinate, especially at median portion, also with a continuous line of appressed setae; surface with dense to contiguous punctation, punctures from large to coarse with strongly curved to appressed setae; prosternal process convex, narrowed distally, basally somewhat enlarged, continuous with prosternal surface, producing a convex region. Mesoventrite convex with coarse punctures, dense to contiguous, also with strongly curved to appressed setae. Metaventrite convex, somewhat flattened along disc, with large to coarse punctures, varying in distribution, sometimes mainly distributed anteriorly, stronger along sides with strongly curved, long to short setae; posterior edge with a fine median projection producing a declivity, projected between metacoxae. ***Genitalia*:** Genital capsule symmetric. Aedeagus symmetric. Phallobase subtriangular, wide to somewhat elongate, with a fine constriction separating anterior and posterior phallobase. Median lobe enlarged and covered by parameres at base; Parameres subparallel, rounded apically; with a V to U-shaped dorsal cross bar.

**Description Female *Size*:** *Total length*. 8.58–10.77 mm. *Total width.* 3.46–4.16 mm. ***Colour:*** as males, sometimes with darker tones. ***Head*:** Shape as males, apparently bigger than males, dorsally more exposed due to reduction in pronotal projection; mandibles symmetric, narrow, only presenting a laminar, longitudinal tooth-like structure along dorsal surface, basally somewhat expanded, dorsal face concave; surface punctate, punctures large to somewhat coarse, mainly densely distributed, with some moderate to sparse areas, also with erect to curved setae, distributed along internal and external surface. ***Pronotum*:** close to males in appearance with less projected anterior angles; pronotal tubercle strongly reduced and transverse, present as a somewhat conspicuous lobe; discal groove shallow; surface strongly punctate, punctures coarse and dense, almost uniformly distributed. ***Elytra*:** as males. ***Legs*:** as present in males with a reduction in meso and metatibiae teeth. ***Venter:*** very close to males except for presenting more conspicuous setae; prosternal process sometimes reduced, almost interrupted by procoxae. Abdominal ventrites similar to males getting narrower distally. ***Genitalia:*** Styli elongate and somewhat wide, rounded apically. External edge of gonocoxites concave distally, becoming convex proximally, anterior portion abruptly narrowed producing a slender projection. Lateral paraprocts forming a C-Shaped plate.

### *3.1.2.2. Psilodon Perty, 1830*

*3.1.2.2.1. = Hexaphyllum Gray, 1832.* **Examined material: *P. schuberti*:Holotype female** (reviewed by photographs) 1♀ (HEC) (Fig. 3b); **Holotype *H. brasiliensis*** 1♂ **(**HEC) (Fig. 3b); **BRAZIL:** Rio de Janeiro, Nova Friburgo A: 1100 m S. Caturama 8.i.1999 E. & P. Grossi leg. 1 ♂ (CERPE); Rio de Janeiro Mun. Resende – Serrinha de Alambari – xii. 2008 U. Caramaschi & H. de Niemeyer col. 1 ♂; Florestinha do Cabo Frio 08/12/1999 (CERPE); Rio de Janeiro. Macaé de Cima Alt. 1500m 28.xii.2000 Isabel Miller leg. 1 ♂ (EPGC); Rio de Janeiro, Nova Friburgo A: 1100 m S. Caturama 3.i.1999 E. & P. Grossi leg.1 ♂ (CERPE); same data except 5.i.1999 1 ♂ (CERPE); same data except 1100m, 15.ii.2009, Interceptação, E. Grossi leg. 1♀ (CERPE); Brasil, RJ, Nova Friburgo 10. i.2001 E. & P. Grossi leg. 1♀ (CERPE); Rio de Janeiro, V. de Mauá, i.97, 1100m, E. & P. Grossi leg 1♀ (CERPE); Nova Friburgo, SESC, Luz, 800m, 19.xii.2008, L.P.C. Grossi leg. 1♀ (CERPE). ***P. westwoodi*: COLOMBIA:** Ibague, Fr. Claver/"Handwriting" Hexaphyllum Brasiliense Grey/Ex. Coll. Boileau 1♂ (MNHN). – ***P. seguyi*: ECUADOR:** Loja iii.2002, P. Arnaud leg. 1♂, 1♀ (CERPE). ***P. xerophilicum*: Paratype BRAZIL:** Encruzilhada, Bahia, xii.1980 A. Martínez & M. Alvarenga leg./"Handwriting" *P. xerophilicum* sp.n Martínez & Reyes C. 1♀ (CERPE); Encruzilhada, 980 m, Bahia, xi.1978, M. Alvarenga leg. 1♂ (EPGC); Encruzilhada, Estr. Torres, 15.xii.2012 1♀ (CERPE); Minas Gerais. Águas Vermelhas, xii.1997, Alt. 850 m A. Bello & F.Z. V. Mello leg. 1♀ (CERPE); Bahia. Ituberá, 11/13.vi.2002, F. Bravo & I. Castro 2♂ (MZUEFS); Bahia, Serra da Jibóia, 12°50′S/39°28′W, 820m 27–28. v.2000, Frerdy leg. 1♂ (MZUEFS). ***P. gilberti*: BOLIVIA:** Nor. Yungas. Caravani-Coroico. xi.2009. 1.800 m. B. Cavelius leg. 1♂ (CERPE). ***P. paschoali*: VENEZUELA:** Altos de Pipe, 12.viii.2011, 1650m, C. Ríos-Málaver leg. 1♂ (CERPE); Miranda, Oripoto, v.2004, 1400 m D. Garcia col. ***P. luki*: Paratypes ECUADOR:** Pichincha Province, Tandayapa (2100 m.a.s.l), ii.2010. legit G. Onore 1♂1♀ (CERPE). ***P. buhrnheimi*: Holotype**: **BRAZIL:** Amazonas, Coari/Rio Urucu, próx. IMT-1,/4°49′33.00″S\ 65°01′49″W,/24–25-ix-1995, 89 m, P.F./Buhrnheim and N.O.Aguiar/BLB [black light bulb] – Pennsylvania 1♂ (CZPB); **Paratype** Amazonas, Guajará,/Ramal do Gama km 12, /07°27′16″/72°38′56″,/06–19.xi.2006, tronco,/F°. [Filho] F. F. Xavier leg. 1♂ (EPCG); Rondônia. Porto Velho. MUIE 9° 33′41.85″S, 65°01′28″W. 02.x.2004, Luminosa M.A.P.A. Silveia leg. 1♂(CERPE); Obidos, Pará, Brasil, x.1938 1♂(MNRJ); **PERU:** Satipo, Junín, Río desconocido 1.2003, 1600 m. R.R. Koike col. 1♂(CERPE). **Not determined species: BRAZIL:** Ceará, Fortaleza**?** Nativas. No more data available 1♂ (CERPE); Goias, São João d'Aliança, 11.xi.1986, 14.7114°S, 47.5161°W, 1000m, R.R. Koike col. 1♂ (EPGC). Espirito Santo, Linhares, P.N. Soretama A: 650m 31.xii.1982 1♂ (EPGC); Espirito Santo Linhares, Caliman Agricola S/A, Sede, 23.x.2003, Luz. P.C. Grossi leg. 1♀ (CERPE); 11/12/99. Linhares Esp. Santo 1♂ (CERPE); RFCVRD, Linhares. Date. 24/11/89 JSS Col. 1♂(CERPE)/same data except Date: 23.11.88 1♂(CERPE); Espirito Santo. Linhares P.N. Soretama A: 650 m F. Z.V. Mello leg. 1♂(CERPE); Espirito Santo, Linhares, RFCVD, 24.xi.1989, A: 700m JSS leg. 1♂(CERPE); Local. Viçosa, Minas Gerais. Data 27/11/82. Col. Martins 1♂(CERPE); Manhu-Mirim. Minas/Col. J. Guerin. S. Paulo. 1♂ (CEAH); Rio de Janeiro, Macaé de Cima 02.i.2002, Altitude: 1600 m, Isabel Miller leg. 1♂ (EPGC); Rio de Janeiro, Nova Friburgo, Macaé de Cima i.2002, 1400 m, I. Miller leg. 1♂ (EPGC); Rio de Janeiro. Petrópolis, Morim, Morro da Bandeira, 1600 m, Torres da Petrobras 02–10.ii.2010 1♂ (CERPE); Rio de Janeiro, Nova Friburgo, A: 1600 m, Cascatinha 1.ii.1999 E. & P. Grossi leg. 1♂ (CERPE); Botucatu, São Paulo, 23.i.1976, Mantovani col. 1♂ (CERPE); Itapema, Santa Catarina, i.1993, Col. J. Carlos. 1♂ (CERPE); Hansa St. Cath. xii.1939/*P. schuberti* (Perty) ♀ P. Pereira det. 1♀ (MNRJ); Hansa, St Cat. xii.1939/Hexaphylum schuberti/*P. schuberti* (Perty) ♂ P. Pereira det. 1♂ (MNRJ); Olho d'Agua, Ponta Grossa, Parana, v.1943/Hexaphylum schuberti (Perty) ♂ P. Pereira det. 1♂ (MNRJ); Santa Catarina, Porto Belo, 28.ii.1961 1♂ (MZUEFS); Itapema Santa Catarina, i.1994, Col. J. Carlos 1♂ (AMBC); Alagoas, Murici, v.1984 D.F. de Moraes Jr. 1♂ (MNRJ). **PARAGUAY:** Pto. Bertoni, Col. Bertoni/*P. schuberti* Pty, AW.B. d., Hexaphyllum Gray./MNHP A.W. Bertoni N – 93 Garcete rev. 1♂ (CERPE). **VENEZUELA:** Monagas State 10°10.332′N, 63°33.315′W, 1110 m, Guachero Cave N.P. 20–21.vii.2010 Holzenthal, Thomson, Cressa, UV lights; VZ10-07-21-02B 1♂ (UMSP); **TRINIDAD AND TOBAGO:** "Handwriting": ? 50/k. ðưððepa/?Hexaphyllum 1♂(ZIN).

**Diagnosis:** Specimens with strong sexual dimorphism in mandibles and pronotum. Males and females with brown to black colour, and dark-red tones in most species. Head anteriorly emarginate, dorsally with a v-shaped excavation along frons, extended anteriorly; vertex convex, concealed under pronotal projection. Labral sufrcae convex with rounded apex, projected between mandibles. Supra-antennal projection variable. Antennae with six to seven lamellae (one species). Eyes conspicuous, strongly developed. Mandibles with an external median tooth (Alpha), sometimes located close to apex forming a concave region (in Andean species), a basal lobe (Beta) and an internal tooth (Gamma). Pronotum projected anteriorly, with a pronotal process covering median surface of head, reduced in females; surface with a longitudinal groove, usually complete, sometimes interrupting females process, punctuation variable, from moderate to coarse, sometimes with shallow excavations and lateral constrictions. Elytra with well-define striae and interstrial costae; humeri not-striate, with tooth-like projections projected

laterally, absent in some Andean species. Anterior tibiae distally enlarged with several strong teeth and tooth-like projections; meso and metatibiae with two to several acute teeth and tooth-like projections, setose, with enlarged apex. Mentum subtrapezoidal. Gula conspicuous and convex, visible on lateral view. Male aedeagi symmetric, phallobase subtriangular, with a strong to somewhat fine anterior constriction, with subparallel to slightly convex sides; median lobe distinctly enlarged basally except for Andean species. Female genitalia with elongate and setose styli, with undivided gonocoxites. Gonoxites abruptly narrowed proximally.

**Description Male.** ***Size:*** *Total length*. 10.29–14.81 mm. *Total width*. 4.34–6.61 mm. ***Colour*****:** Body entirely black to somewhat brown, often with dark-red tones. ***Head*****:** Shape transverse, emarginate; labral surface smooth, elongate, convex to somewhat flattened in some species, rounded at apex with a tuft of conspicuous setae; anterior margin with shagreened surface, somewhat carinate, glabrous; frons slightly excavate; vertex concealed, covered by anterior portion of pronotum. Mentum trapezoidal with a somewhat lobed anterior edge, with few large to coarse punctures, also with yellowish curved setae. Gula conspicuous, strongly convex, sub-trapezoidal to oblong, easily visible in lateral view, surface strongly and almost entirely carinate, carina smooth, sometimes with sparse fine punctuation. Gena with coarse to large punctures, dense, with yellowish, strongly curved to appressed setae. Mandibles symmetric, with a median to subapical tooth (Alpha), a basal internal tooth (Gamma) and a basal lobe (Beta); strongly curved inwards and directed upwards apically; base of mandibles enlarged in most species, producing a dorsal surface, reduced in Ecuadorian species. Antennae with six or seven lamellae. ***Pronotum*****:** shape convex, anterior margin projected anteriorly, with a convex, and frequently conspicuous tubercle; posterior margin sinuate; anterior angles reaching posterior portion of eyes; discal groove present, shallow to deep; surface with moderate, large or coarse punctures, dense to contiguous, sometimes with two to four distinct excavations; lateral pronotal carina distinct, separating disc from hypomeron, complete and continuous with posterior and anterior margins, except at anterior projection, with a somewhat scalloped surface, and minute simple setae. ***Elytra*****:** Elytral humeri not striate, with or without a tooth-like projection, mostly present in Brazilian species; surface strongly punctate with well-defined striae; striae with coarse punctures and minute setae; interstriae forming longitudinal costae with moderate to large and dense to contiguous punctuation; epipleuron complete to apex, concave to somewhat flat, with dense to contiguous punctuation, large or coarse basally, becoming moderate at apex; elytral apex with a interstrial, convex joint. ***Legs:*** all tibiae serrate, with stronger and higher number of teeth at protibiae; meso and metatibiae with few strong teeth, normally varying from three to four well-defined teeth, always with several tooth-like projections, sometimes with two serrate lines along external portion of tibiae; apex enlarged with tooth-like projections. ***Venter*****:** Prosternum carinate along anterior and posterior margins; with a convex, somewhat conspicuous process; surface with coarse to large punctures densely distributed. Mesoventrite convex, with contiguous to dense coarse punctuation and conspicuous appressed setae. Metaventrite distinctly convex, medially somewhat smooth, frequently with conspicuous appressed setae; lateral portions with coarse to large punctuation, dense to sparsely distributed; discrimen not present as a narrow groove, instead present as a complete or incomplete superficial one, with a declivity at posterior end. Abdominal ventrites with fine, dense to contiguous punctuation, sometimes with moderate to large punctuation across posterior margins; porterior margin of I-IV ventrites with a transverse carina; last ventrite with conspicuous setae at apex. ***Genitalia*****:** Genital capsule symmetric; dorsally divided into three regions, discal plate sub-trapezoidal, distally almost truncate; dorso-lateral plates sub-triangular, but extending anteriorly as a single strut with sharp apex; ventral plate transverse to oblong, becoming narrower anteriorly, forming a single strut at proximal portion; distal edge rounded to almost truncate, surface with simple appressed setae, densely distributed, projected to median axis. Aedeagus symmetric, with subparallel sides; shape from strongly elongate (approx. 4.0X longer than wider) and narrow to moderately elongate (approx. 2.5X longer than wider). Anterior and posterior phallobase divided by a strong constriction forming two well-defined regions. Anterior phallobase rounded apically, varying from sub-trapezoidal to subtriangular shape. Posterior phallobase with almost subparallel sides, also with slightly convex to somewhat concave sides. Parameres with straight sides in most species, on lateral view from strongly to slightly concave, apically rounded. Median lobe enlarged at base, gradually narrowed apically; when Aedeagus strongly elongate penis slender.

**Description Female:** ***Size*****:** *Total length.* 11.51–15.27 mm. *Total width.* 4.49–6.54 mm. ***Colour:*** as males. ***Head:*** shape as males, size bigger than males head, more visible on dorsal view, anteriorly emarginate; vertex somewhat excavate; mandibles symmetric, narrow, distinctly different from males, almost straight, concave at dorsal portion, without teeth, instead with a longitudinal external carina from base to apex maxillary and labial palps shorter when compared with males; surface punctate, mainly basally, punctures large to somewhat coarse, denser at base, getting sparse distally, with simple, erect to slightly curved yellowish setae. ***Pronotum*****:** as males but presenting less distinct anterior angles; anterior edge less projected anteriorly; also with a considerable reduction in pronotal tubercle, with sub-trapezoidal shape on dorsal view; discal groove deep, often complete to apex, sometimes reaching pronotal process dividing it in two portions. ***Elytra*****:** as males. ***Legs:*** as males except for presenting subequal and smaller apical spurs at meso e metatibiae. ***Venter:*** very close to males except for presenting more conspicuous setae; prosternal process sometimes reduced, almost interrupted by procoxae. Abdominal ventrites similar to males getting narrower distally. ***Genitalia:*** Styli elongate and setose, with undivided and somewhat convex gonocoxites, showing almost the same width except proximally where each gonocoxite is abruptly narrowed, producing a slender projection. Lateral paraprocts enlarged proximally, rounded with globous to somewhat "C" shaped.

### *3.1.3. Comparative remarks on Syndesus and Psilodon*

Given the strong resemblance between both genera it is difficult to determine the limits between them. It is also hard to identify good diagnostic traits at species and generic level due the intraspecific variation of some characteristics, such as the presence of species with six or seven lamellae in both genera, fine variations in mandibular teeth, elytral humeri, interstrial costae, metaventrital disc and some genitalic characteristics in both males and females. First of all it is important to summarize the main shared traits by *Syndesus* and *Psilodon*, which can define Syndesini MacLeay, 1819: Strong sexual dimorphism. Head emarginate, dorsal surface partially concealed by pronotum, medially excavated forming a "V" shaped region. Clypeus indistinct, instead with an intermandibular projection between mandibles. Labrum dorso-ventrally projected between mandibles, with rounded to truncate apex. Gula conspicuous, strongly convex and almost entirely glabrous. Eyes conspicuous, almost entirely extended through sides. Male mandibles strongly to somewhat curved inwards; dorsally curved in females. Pronotal antero-lateral angles rounded to oblique, anteriorly with a variable in shape tubercle, reduced in females; lateral pronotal carina present and complete, with scalloped surface. Elytra with well-defined striae and variable number of interstrial costae; epipleuron somewhat concave, abruptly narrowed basally, complete to apex. Legs serrate, with stronger teeth at protibiae. Meso and metatibie acute teeth and tooth-like projections. Prosternal process narrow. Meso and metaventrite finely to strongly convex abdominal ventrites with fine and contiguous to densely distributed punctuation, also with a transverse carina along posterior margin of every ventrite.

Based on the previous characters is possible to describe the principal differences between *Syndesus* and *Psilodon*. The sexual dimorphism is present in the same structures but *Syndesus* shows differences between male and female lamellae, being finely reduced in females. Male mandibles are probably the main difference between both genera, in

**Table 2**
Comparison between mean square values of error components from Procrustes ANOVA of all analysed traits. Individual error are higher in all cases.

| | RMM | LMM | PT | DFP | DFE |
|---|---|---|---|---|---|
| **Individual Error** | 0.0020859548 | 0.0020637583 | 0.0015946985 | 0.0006454029 | 0.000094667 |
| **Total Error** | 0.0002147154 | 0.0000113199 | 0.0000318851 | 0.0000711143 | 0.0000260213 |

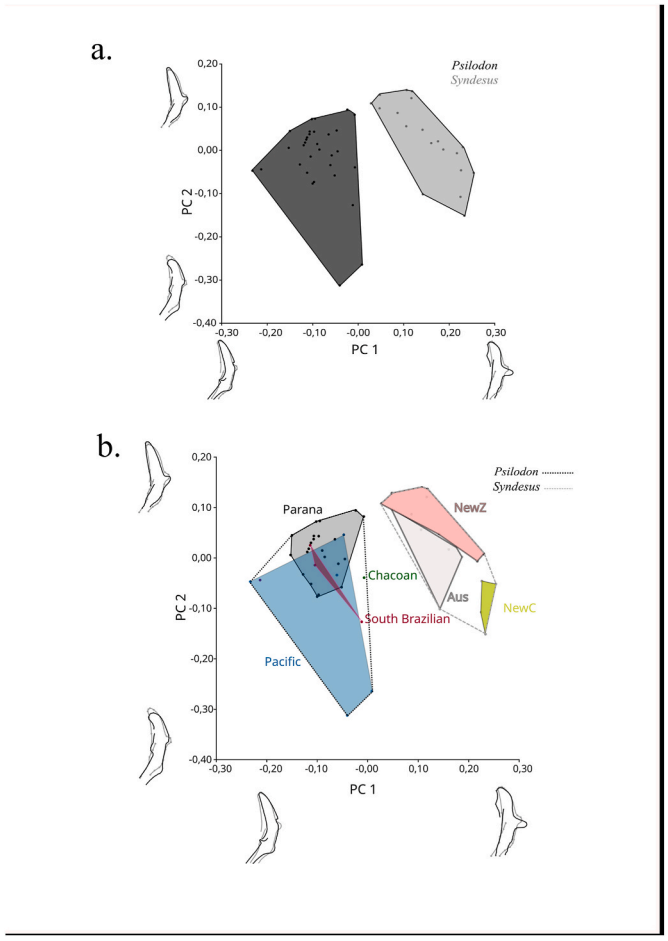


**Fig. 5.** Principal component analysis (PCA) of the shapes of the right mandible of males (RMM), calssified by **a)** *Genus*, and **b)** the biogeographic dominions of Neotropical and Australasian regions.

Australasian species, mandibles only present one strong external tooth and a laminar one across internal face, extended from base to apex, in New Caledonian this tooth is antero-posteriorly constricted producing a tooth-like projection. In *Psilodon* species male mandibles show a basal enlargement, forming a narrow dorsal surface, this trait allows the presence of a basal internal tooth, defined by Didier (1929) as the γ (Gamma) tooth, a basal, external β (Beta) lobe, and a median to sub-apical external α (Alpha) tooth, being this one the strongest.

### 3.2. Geometric morphometrics analyses

The values of the mean squares from Procrustes ANOVA showed to be lower for the error component of variation than the individual component in every analysed trait (*IndividualError* > *TotalError*) (Table 2), discarding definition errors for the proposed Landmarks.

#### 3.2.1. Right male mandible comparison

Most of the total shape variation for **RMM** (Fig. 5a and b.) was explained by de PC 1 (40.388%), which clearly separate two well-define clusters for each Syndesini genus. The PC2 explained 18.839%, showing an apparent influence separating the species examined. According to the results mandible curvature do not seems to have a strong influence over shape variation, on the other hand, mandible apex (LM: 10–13), alpha (LM: 6–9) and gamma (LM: 15–19) teeth shape and presence or absence of beta lobe (LM: 2–5) have a strong influence on PC scores. *S. cancellatus* represents the highest score across PC1 (0.254), such value responds to a strongly truncate apex, the absence of beta lobe, reducing basal expansion of mandible, the strong alpha tooth located medially and the unique configuration of gamma tooth, which is present as a laminar tooth extended from base to apex. Changes in mandibular shape of *Syndesus* species also seem to respond to the upwards projection of internal face involving LM: 14–20. The lowest score of PC1 (−0.233) was define by the Ecuadorian species *P. luki*, this values are presumably related with the presence of an acute apex, producing narrower mandibles when compared with New Caledonian species, it also responds to the preapical position and almost perpendicular orientation of alpha tooth, a reduction in the basal expansion due to the fusion of gamma tooth and beta lobe, a typical trait of the Ecuadorian *Psilodon*. In general terms the mandibular shape variation of *Psilodon* species responds to a narrower surface represented by a reduction of the distances between the continuous line of LM: 1–9 and the internal line of LM: 14–20, this configuration produces a uniformly concave internal face of mandibles, making it less exposed from dorsal view.

Shape variation through PC2 presents a less abrupt variation, but morphological changes respond to similar patterns, as is the case of mandibular apex, being rounded to somewhat truncate at the lowest value (−0.312), represented by *P. westwodi*, which also presents the more conspicuous configuration of gamma tooth represented by antero-lateral projection of LM: 14–19. The distribution of the internal landmarks produces a clear basal dorsal surface, followed by the strong internal projection of gamma tooth and a uniform concave region apical, perpendicular in relation to gamma tooth. The highest score of PC2 (0.140), defined by one specimen of *S. cornutus,* is not represented by a strong variation of landmark distribution, and as is the case of the other specimens from the Australasian region, the basal configuration of external (1–9) and internal (14–20) landmarks allows a high exposition of internal face from dorsal view.

Using as the main classifier the *biogeographic dominion* (Fig. 4b.), we can observe a somewhat a well-define cluster for the Parana dominion, with close PC scores showed by the only record from the Chacoan dominion, and superposition with two specimens from the South Brazilian one (2 males of *P. burnheimi*). The other record from the South Brazilian dominion was represented by the Bolivian Yungas specimen: *P. gilberti* registered a score closer to the Pacific dominion values. The remaining specimens distributed along the Pacific dominion showed highly variable scores mainly influenced by PC2, with the lowest scores represented by *P. westwoodii* from Colombia and an undetermined species from Venezuela. It is interesting that the two records of *P. paschoali*, a species with distribution data from Colombia and Venezuela registered PC scores (record 1: PC1: −0.061; PC2: −0.034/record 2: PC1: −0.047; PC2: 0.046) with high superposition with the Parana dominion.

The pairwise distances of the Discriminant Analysis for RMM showed to be significant for Mahalanobis distances (P: 17.57, $p < 0.0001$) and Procrustes distances (P: 0.2452, $p < 0.001$) using *genera* as classification criterion. The comparison of Mahalanobis distances through the *biogeographic dominions* CVA (see Table 3) showed significant differences within the Australasian dominions, however, Procrustes distances only registered significant differences between New Zealand (*S. cornutus*) and New Caledonian (*S. cancellatus* and *S. punctatus*) species. Neotropical

**Table 3**
p-values from permutation tests (10 000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **RMM**. Significant differences: p < **0.01**.

| | Australia | Chacoan | New Caledonia | New Zealand | Pacific | Parana |
|---|---|---|---|---|---|---|
| Chacoan | 0.0336/*0.2022* | | | | | |
| New Caledonia | **0.0073**/*0.0200* | 0.0483/*0.1993* | | | | |
| New Zealand | **<0.0001**/*0.0580* | 0.0177/*0.0827* | **0.0002**/***<0.0001*** | | | |
| Pacific | **<0.0001**/*0.0161* | 0.0239/*0.6684* | **0.0077**/***0.0080*** | **<0.0001**/***0.0001*** | | |
| Parana | **<0.0001**/***<0.0001*** | 0.0402/*0.0351* | **<0.0001**/***<0.0001*** | **<0.0001**/***<0.0001*** | **<0.0001**/***0.0077*** | |
| South Brazilian | **0.0088**/*0.0591* | **<0.0001**/*0.5040* | 0.0153/***0.0061*** | **0.0009**/***0.0008*** | **0.0023**/*0.07175* | **<0.0001**/*0.1093* |

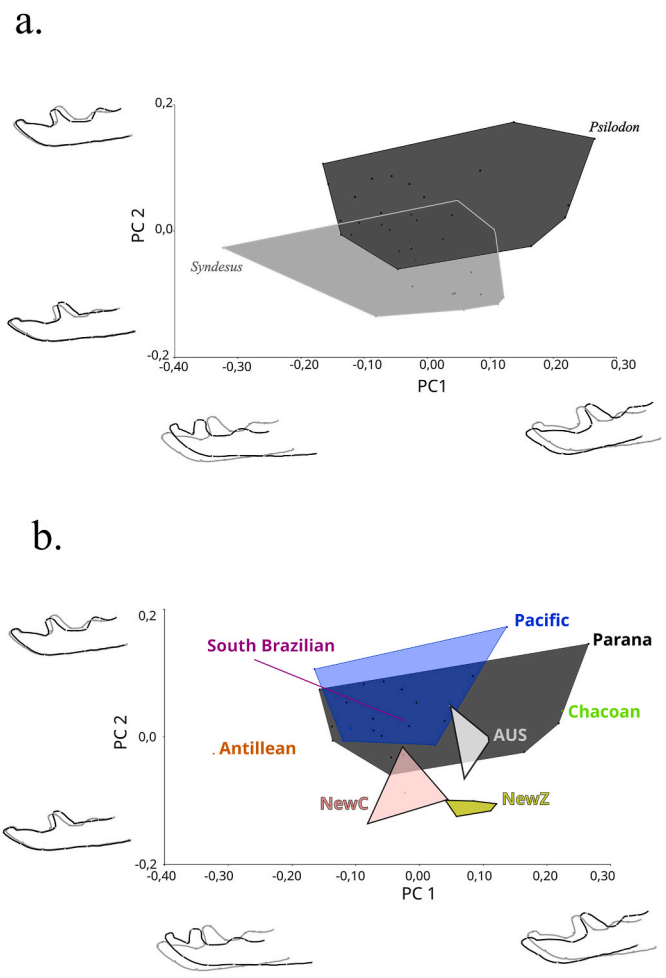


**Fig. 6.** Principal component anlysis (PCA) of the shapes of the lateral view of the left mandible of males (LMM) classified by **a)** *Genus*, and **b)** the biogeographic dominions of Neotropical and Australasian regions.

dominions showed a similar pattern, presenting significant differences between Mahalanobis distances of most dominions except between Pacific and Chacoan, and Parana and Chacoan. In regard to Procrustes distances there were only registered significant differences between Parana and Pacific dominions. When comparing the Neotropical Australasian dominions there were recorded significant differences between most comparisons of Mahalanobis and Procrustes distances (Table 3), except among Chacoan and Australasian ones.

### 3.2.2. *Left male mandible (on lateral view) comparison*

The 44.627% variation of **LMM** was explained by PC1, and PC2 explained the 17.282% (Fig. 6a. And b.). While PC1 appeared to facilitate the separation among species, PC2 showed to influence the separation between *Syndesus* and *Psilodon*. The lowest score along PC1 (−0.32), represented by the Dominican fossil *S. ambericus* Woodruff, 2009, responds to a strong variation at mandibular apex where alpha tooth (LM: 9–13) presents a preapical position and an almost perpendicular orientation, it also seems to be related to a reduction between landmarks 7 and 8 which produced a narrower mandibular apex in relation to the other examined specimens.

The highest score recorded for PC1 (0.27) represented by an undetermined species of Brazilian Atlantic Forest is related with the median location of alpha tooth (LM: 9–13), presenting a higher distance from LM: 8 when comparing with *S. ambericus*. There is also a strong shape variation regarding apical landmarks (6–9) that are projected anteriorly and presents a distinct configuration that produces a wider mandibular apex. Median scores respond to changes on alpha tooth represented by fine migrations (closer or not to apex) and orientation, from almost perpendicular to anterodorsally projected. Variation along PC2 is related with changes on the distances between the ventral (LM: 1–7) and the dorsal (LM: 8–17) line of landmarks, producing narrower mandibular shapes at low scores and wider ones at higher scores. There is also a strong influence represented by beta lobe (LM: 14–17) variation, entirely absent in *Syndesus*, producing a flat region and a dorsal projection of landmarks 15 and 16 in *Psilodon*, which produce a convex region.

PCA failed to produce a clear separation between the Neotropical and Australasian dominions, showing a fine separation through PC2 between New Zealand and New Caledonian specimens Neotropical taxa. Australian specimens registered a high superposition with Parana dominion. PC1 showed a clear separation between LMM shape of *S. ambericus*, from the Antillean province and the remaining specimens.

The pairwise distances of the Discriminant Analysis for LMM was significant for Mahalanobis (P: 14.6380, $p < 0.0001$) and Procrustes distances (P: 0.1265, $p$ 0.0009) under the criterion *genus*. Using the *biogeographic dominions* as the main classification criterion for CVA

**Table 4**
p-values from permutation tests (10 000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **LMM**. Significant differences: p < **0.01**.

| | Australia | Antillean | Chacoan | New Caledonia | New Zealand | Pacific | Parana |
|---|---|---|---|---|---|---|---|
| Antillean | **<0.0001**/*0.1794* | | | | | | |
| Chacoan | **0.0858**/*0.1363* | **<0.0001**/*1.000* | | | | | |
| New Caledonia | **<0.0001**/*0.0182* | 0.1809/*0.1981* | 0.1828/*0.0318* | | | | |
| New Zealand | **0.0036**/***0.0098*** | **<0.0001**/*0.0164* | 0.0104/*0.1340* | **0.0016**/***0.0006*** | | | |
| Pacific | **0.0018**/*0.0114* | 0.1696/*0.3109* | 0.1267/*0.1114* | **0.0011**/***0.0084*** | **0.0006**/<0.0001 | | |
| Parana | **0.0001**/*0.0217* | 0.0474/*0.0763* | **0.0013**/*0.0882* | **0.0002**/***0.0062*** | **<0.0001**/***0.0021*** | **<0.0001**/*0.0762* | |
| South Brazilian | 0.1901/*0.4044* | **<0.0001**/*1.0000* | **<0.0001**/*1.0000* | 0.0351/*0.3945* | 0.0367/*0.0905* | 0.1567/*0.9972* | 0.0268/*0.9344* |

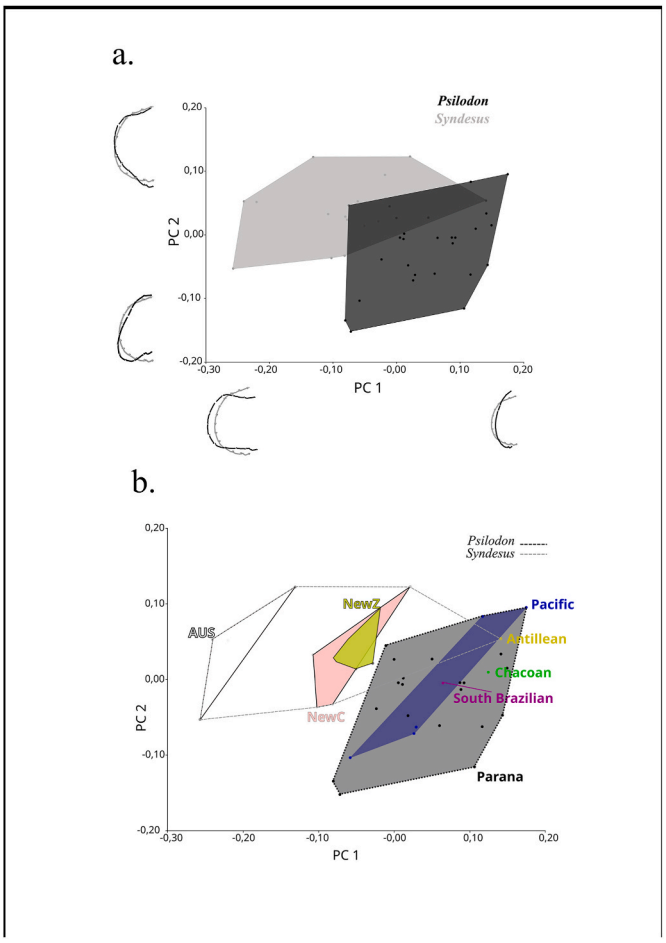


**Fig. 7.** Principal component anlysis (PCA) of the shapes of the lateral view of the pronotal tubercle of males (PT) classified by **a)** *Genus*, and b) the biogeographic dominions of Neotropical and Australasian regions.

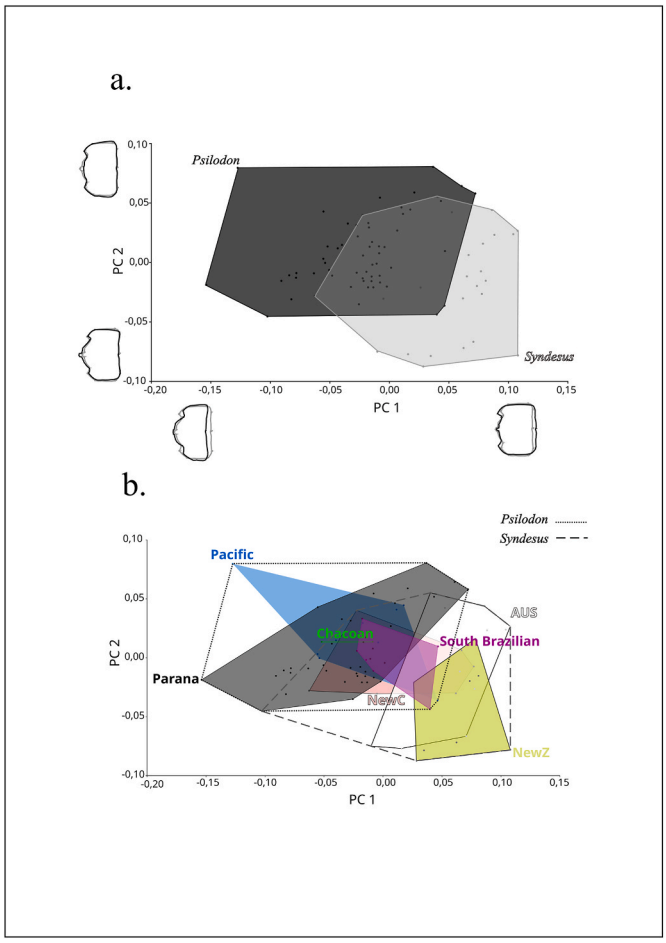


**Fig. 8.** Principal component anlysis (PCA) of the shapes of the dorsal face of pronotum (DFP) classified by **a)** *Genus*, and **b)** the biogeographic dominions of Neotropical and Australasian regions.

(Table 4.), Mahalanobis and Procrustes distances were significant between most comparisons involving Australasian and Neotropical dominions, being the South Brazilian one, the only which not registered significant differences between New Zealand, New Caledonian and Australian specimens.

### 3.2.3. *Pronotal tubercle comparison*

The PCA for **PT** shape (Fig. 7a and b) successfully represented the shape variation between *Syndesus* and *Psilodon*. PC 1 represented the 62.647% and PC 2 the 22.990% of the total variance. It was possible to obtained two well-defined clusters, one represented by *Syndesus* species and Australasian dominions, and another for the Neotropical genus *Psilodon*. The superposition of both clusters along the PC1, was mainly given by the *S. ambericus* fossil score (0.14) from the Antillean dominion, whose shape is closer to *Psilodon* species, showing less projected landmarks (LM: 4–11) anteriorly, and a typical dorsal projection represented by LM: 11–13, only presented in the studied specimens from North-East Venezuela and Trinidad and Tobago.

The pairwise distances of the discriminant analysis of **PT** showed significant differences for both Mahalanobis (P: 3.978, $p < 0.0001$) and Procrustes distances (P: 0.1463, $p < 0.0001$), which are the result of strong differences between *Syndesus* and *Psilodon* PT projection, which is clearly stronger in all *Syndesus* specimens, represented by LM: 2–12.

In regard to the *biogeographic dominions* comparison, there were recorded significant differences between most Australasian and Neotropical Mahalanobis distances. It is interesting to point out that *Syndesus* fossil from Dominican Republic shows differences from the Australasian members of the genus, differences that are also present between Parana and Pacific Neotropical dominions.

There were only identified significant differences between the

**Table 5**
p-values from permutation tests (10 000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **PT**. Significant differences: p < **0.01**.

| | Australia | Antillean | Chacoan | New Caledonia | New Zealand | Pacific | Parana |
|---|---|---|---|---|---|---|---|
| Antillean | **<0.0001**/*0.0984* | | | | | | |
| Chacoan | **<0.0001**/*0.0842* | 1.000/*1.000* | | | | | |
| New Caledonia | **0.0004**/*0.0533* | **<0.0001**/*0.1810* | 0.1484/*0.1993* | | | | |
| New Zealand | **0.0022**/*0.7213* | 0.1079/*0.1062* | 0.0853/*0.0328* | **0.0025**/***0.0018*** | | | |
| Pacific | **0.0063**/*0.1281* | **0.0018**/*0.8319* | 0.1606/*0.8281* | **0.0010**/***0.0071*** | **0.0023**/***0.0040*** | | |
| Parana | **<0.0001**/*0.0107* | 0.0349/*0.1718* | **0.0026**/*0.4604* | **<0.0001**/**<0.0001** | **<0.0001**/***0.0008*** | **0.0008**/*0.5051* | |
| South Brazilian | 0.0784/*0.2633* | **<0.0001**/*1.000* | 1.0000/*1.0000* | 0.0168/*0.2015* | 0.1190/*0.0701* | 0.0861/*1.0000* | **0.0046**/*0.9745* |

**Table 6**
p-values from permutation tests (10 000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **DFP**. Significant differences: p < **0.01**.

| | Australia | Chacoan | New Caledonia | New Zealand | Pacific | Parana |
|---|---|---|---|---|---|---|
| Chacoan | **0.0037**/*0.0363* | | | | | |
| New Caledonia | **0.0004**/*0.2945* | **0.0073**/*0.1466* | | | | |
| New Zealand | **<0.0001**/*0.1471* | 0.0148/*0.0511* | **0.0006**/*0.2721* | | | |
| Pacific | **<0.0001**/**<0.0001** | 0.0386/*0.3875* | **0.0007**/*0.0973* | **<0.0001**/***0.0002*** | | |
| Parana | **<0.0001**/**<0.0001** | 0.8052/*0.9751* | **<0.0001**/*0.0028* | **<0.0001**/**<0.0001** | **<0.0001**/***0.0062*** | |
| South Brazilian | **<0.0001**/***0.0029*** | 0.4233/*0.4801* | **0.0001**/*0.0607* | **0.0002**/***0.0012*** | **<0.0001**/*0.0551* | **0.0028**/*0.0880* |

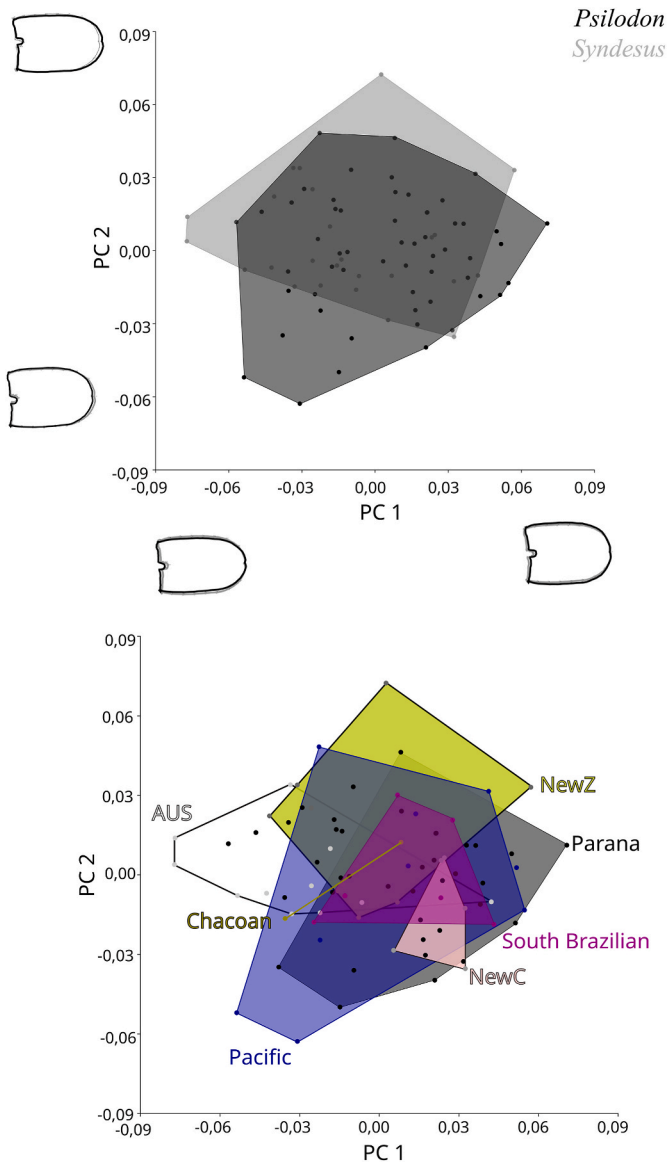


**Fig. 9.** Principal component anlysis (PCA) of the shapes of the dorsal face elytra (DFE) classified by **a)** *Genus*, and **b)** the biogeographic dominions of Neotropical and Australasian regions.

Mahalanobis distances (Table 5.) of Antillean-Australia, Chocoan and Parana; Antillean-New Caledonia and South Brazilian; New Caledonia-Parana; New Zealand Parana. In the case of Procrustes distances for the same criterion it was only possible to observe significant differences between New Caledonia and Parana dominions. There were not significant differences of Procrustes distances within Neotropical dominions.

### 3.2.4. *Dorsal face of pronotum comparison*

PCA for **DFP** (Fig. 8a and b.), two somewhat well-defined clusters for each genus. PC 1 explained the 37.467% and PC 2 the 16.725% of the total shape variation. Despite the high superposition it was possible to perceive the strong influence of LM: 1–5 and 11–14 along the anterior margin of the pronotum. As it was observed for **PT**, the shape variation was influenced by changes in the projection degree. **DFP** showed a similar pattern, with the lowest scores along PC1 (−0.15 and 0.13) representing a strong anterior projection of LM: 1–3 and 13,14, which form a convex region including the pronotal tubercle, present in *P. xerophilicum* and the *Psilodon* specimen from Trinidad and Tobago. The shape variation in this cases is also influenced by a regression of LM: 4 and 12, reducing the projection of antero-lateral angles of the pronotum. With higher scores (e.g. 0.10) of PC 1, the general shape of the pronotum becomes subquadrate with a clearly reduction in anterior projection of the anterior margin, represented by *S. cornutus* specimens. Variation along PC 2 showed similar patterns to PC1, with low scores influenced by a strong projection of pronotal tubercle characteristic of *Syndesus* species, becoming less projected at higher scores, which show the typical shape of most *Psilodon* species.

The pairwise distances of the discriminant analysis performed for **DFP**, showed sigjnificant differences between Mahalanobis (P: 4.7692, $p < 0.0001$) and Procrustes (P: 0.0851, $p < 0.0001$) distances of *Syndesus* and *Psilodon*. When using as classifier the *biogeographoc dominions* (Table 6) we obtained significant differences between most Mahalanobis and Procrustes distances from Australasian and Neotropical dominions, suggesting a strong influence of the biogeographic component. It was also possible to identify significant differences in pronotal shape variation between most *Psilodon* specimens distributed across different biogeographic dominions (see Table 6).

### 3.2.5. *Dorsal face of elytra comparison*

PCA for **DFE** (Fig. 9a and b.) failed to separate both *genera* and *biogeograohic dominions*, resulting in a high data superposition. The PC 1 represented 41.4% of the total variation and PC2 the 22.2%. The pairwise comparison under the criterion *genus,* showed to be significant for Mahalanobis distances (P: 3.871; $p < 0.001$), but not for the Procrustes ones (P: 0.0218; $p$ 0.0127). Shape differences responds tu a reduction in distance between LM 1–2, and 20–21 which results in a more cylindrical elytral shape at low PC scores (*Syndesus* species), and a more robust one for higher scores (*Psilodon* species). For *biogeographic dominions* (see Table 7), Mahalanobis distances showed significant differences between Australasian and Neotropical dominions, there were also recorded differences within regions, suggesting a specific elytral shape for almost every analysed biogeographic dominion.

## 4. Discussion

With this study it was possible to identify a significant variation for mandibular, pronotal and elytral shape between the two genera currently positioned in Syndesini. Using geometric morphometrics and strict taxonomic comparisons, this research offers now a strong support to define the limits between the Australasian and Neotropical members of this Syndesinae tribe.

The diagnostic traits identified through the taxonomic evaluation,

**Table 7**
p-values from permutation tests (10 000 permutation rounds) for Mahalanobis (normal font) and Procrustes (*Italic*) distances among Biogeographic Dominions for **DFE**. Significant differences: $p < \mathbf{0.01}$.

| | Australia | Chacoan | New Caledonia | New Zealand | Pacific | Parana |
|---|---|---|---|---|---|---|
| Chacoan | **0.0014**/*0.4018* | | | | | |
| New Caledonia | **<0.0001**/*0.018* | 0.0334/*0.0264* | | | | |
| New Zealand | **<0.0001**/*0.0467* | **0.0056**/*0.6334* | **0.0006**/***0.0071*** | | | |
| Pacific | **<0.0001**/***0.0074*** | 0.0132/*0.8181* | **0.0006**/*0.2476* | **<0.0001**/*0.166* | | |
| Parana | **<0.0001**/**<0.0001** | **0.0003**/*0.5260* | **<0.0001**/*0.0639* | **<0.0001**/*0.0631* | **<0.0001**/*0.1740* | |
| South Brazilian | **<0.0001**/**0.0159** | 0.0339/*0.5042* | **0.0017**/*0.2986* | **0.0004**/*0.3302* | **0.0001**/*0.7083* | **<0.0001**/*0.9665* |

mainly represented by strong shape variations at male mandibles and male and female pronotum and pronotal tubercle, were consistent with the geometric morphometrics analysis results. Changes among these structures are difficult to describe, as it is hard to define good reference points which reflect its relative position, size and shape. This is specially true for the teeth position along male mandibles, and also the shape and degree of projection of pronotal tubercle, and pronotal antero-lateral angles. In these cases, geometric morphometric techniques showed to be highly effective in assisting the taxonomic descriptions, which with the other studied traits, offer a well-supported and less subjective description.

Previous works involving geometric morphometric methods within Lucanidae, studied the shape variation of similar body structures used in this work, showing to be effective for the evaluation of allometric patterns and sexual dimorphism of different Lucaninae genera such as *Prosopocoilus* (Tatsuta et al. 2004), *Chiasognathus* (Vergara et al. 2014), *Colophon* (Eldred et al. 2016), *Lucanus* (Romiti et al. 2016), and *Odontolabis* (Matsumoto & Knell 2017). With our study, we show that geometric morphometrics are also useful to resolve taxonomic inconsistencies.

The examples cited above, as most Lucanidae studies, are centred in Lucaninae. This is the first study in which a geometric morphometric dataset for Syndesini is offered, as the only available data regarding Syndesinae was provided by Zhang et al. (2019), and only included Ceruchini Jacqueline Du Val and Fairmaire, 1859 and Sinodendrini Mulsant, 1842 in their evolutionary study. The absence of *Syndesus* and *Psilodon* in this study, reflects not only its under-representation in most entomological collections, but also the limitations concerning evolutionary interpretations within the subfamily, as the Ceruchini and Sinodendrini morphologies are considerably different from Syndesini, suggesting a clear separation between the Holarctic and Austral Syndesinae, which has not been studied so far.

Additionally to the morphological comparisons at generic level, the same comparisons were also conducted from a biogeographic approach using biogeographic dominions as the comparative factor. Due the lack of larger series of specimens for each dominion, biogeographic interpretations are to some extent limited at this level, however, if we consider the results from a regional perspective, the statistical differences between the shape data (Mahalanobis and Procrustes distances) from the Neotropical and Australasian regions, it is possible to support the existence of at least, two Syndesini genera instead of one.

Burmeister (1847a) and Arrow (1938) stated that considering *Syndesus* and *Psilodon* as synonyms, would represent and unnatural separation, given the strong morphological resemblance presented by both taxa. With the modern theory of vicariance, all taxonomic hypothesis should be proposed from an evolutionary perspective. In the case of all taxa studied in this work it is important to consider that the connections between South America and Austrailia were interruped at the Cretaceous, around 65 MYA (Grimaldi & Engel 2005). Woodruff (2009), supported this observations when he described *S. ambericus* fossil, stating that considering *Syndesus* and *Psilodon* as synonyms, would totally ignore the biogeographical influence in taxa divergence processes. In spite of this, Woodruff decided to place the fossil species in *Syndesus*, which presents a closer morphological resemblance with *Psilodon* species.

Considering the separation between the Syndesini genera, it is now possible to hypothesize about the biogeographic history of the tribe, suggesting a Gondwanan origin inferred from the results obtained by Paulsen (2013) and Kim & Farrell (2015) for other Stag Beetles genera such as *Casignetus* MacLeay, 1819; *Chiasognathus* Stephens, 1831; *Streptocerus* Dejean, 1833; *Sphaenognathus* Buquet, 1838; *Hilophyllus* Paulsen and Mondaca, 2006, among others which, together with their related Australasian taxa, conforms tribes as Lamprimini MacLeay, 1819; Chiasognathini Burmeister, 1847b; Ceratognathini Sharp, 1899 and Casignetini Reid, 1999. Similar patterns have been registered for other beetle taxa, as is the case of *Araucaria*-associated bark beetles (Sequeira & Farrell 2001), water scavenger beetles (for West Gondwana vicariance) (Toussaint et al. 2017), and ground beetles (Sota et al. 2022).

## 5. Conclusions

With our results we establish the basis for defining the limits between both Syndesini genera, with *Syndesus* including the four species restricted to the Australasian region and *Psilodon* with the eight species from the Neotropical region. Given the limitations related to the lack of available material, especially for *Syndesus* species, to offer more robust results, further efforts must be focused on collecting new material, mainly for the obtention of DNA samples, which would help to clarify the evolutionary relationships within Lucanidae. While conducting our study we observed several undetermined species of *Psilodon*, which remarks the need for a taxonomic revision.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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