Passalopalpidae, a new family from the Cretaceous Burmese amber, as the possible sister group of Passalidae Leach (Coleoptera: Scarabaeoidea)

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ABSTRACT

A new family of Scarabaeoidea is revealed from the Cretaceous amber of Myanmar (earliest Cenomanian, near 100 Ma), on a series of males and females, most in perfect condition. Passalopalpidae fam. nov., Passalopalpus cheni gen. et sp. nov., are probably extinct since a long time. Observations were made on the whole body (head, thorax, abdomen) and appendages (mouthparts, antennae, legs, wings). Most characters are remarkable and plesiomorphic, compared to Passalidae Leach, as well as to some other Scarabaeoidea. Morphological characteristics demonstrate that the fossil species is typically « passaloid », but that it cannot belongs to Passalidae. Passalopalpidae and Passalidae are clearly distinct families, with strong assumption to be sister groups. The systematic interpretation of the fossil could fill a historic gap: the sister group of Passalidae had been established previously never in a solid way. Passalids are Gondwanian, whereas passalopalpids lived on former eastern Laurasia. Vicariance of both taxa, each on one of the super-continents, seems to support recent hypotheses of phylogeny and paleobiogeography for Passalidae. Other preliminary notes are given on the morphology, biology and phylogenetic relationships of passalopalpids.

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1. Introduction

Passalidae form an outstandingly homogeneous group, immediately recognizable amongst Scarabaeoidea. More than 700 species were described, but there would be in a whole thousand (Boucher, 2006). Their geographical distribution is pantropical and is in narrow relation with rainforests. They live and consume rotten wood and therefore, except rare instances, are saproxylophagous. Their subsocial behavior is peculiar in the order Coleoptera. After grouping of the only true passalids (mainly since Westwood, 1834), the family contains two distinct subfamilies — Passalinae and Aulacocyclinae Kaup — and has been established as a monophyletic group (Boucher, 2006). For this author, the family would have spread and diversified following the only Gondwanian drift. Today each continent contains only one or several tribe(s). This endemism has probably for origin ecological constraints: species inhabit permanently a very stable environment; they move little because of their behavior and microhabitats. Consequently, the current distribution of higher taxa of passalids on each continent results from passive dispersals by terrestrial way from the wet forest tropical belt.

Passalinae are pantropical, with five tribes, as revised by Boucher (2006): Passalini, Proculinia Kaup, Solenocyclini Kaup, Leptaulacini Kaup and Macrolininia Kaup, whereas Aulacocyclinae are exclusively Indo-Australasian, with two tribes: Aulacocyclini and Ceracupini Boucher. Such geographical distinction is fundamental in the phylogenesis of the tribes of the family. Passalinae spread in America, Africa-Madagascar, on the Indian Peninsula, in insular and continental Asia, on a part of Micronesia and Melanesia, and in Australia. Aulacocyclinae are considered as originating from Australia and they doubtless never occurred in Africa and even less in America. The
known fossils of Passalidae are not so old and close to current taxa: *Passalus indormitus* Cockerell (a Passalini from North American Oligocene) and *Serrulus sinicus* Hong (a Macrololini from continental Chinese Miocene). The study of an older fossil, from the Santana Formation, Brazil, Lower Cretaceous, and interpreted at first by R.A. Crowson as a possible Passalidae (Grimaldi, 1990), showed that it is not a taxon of the family, nor probably of a nearby family (details in Boucher, 2006). The absence of Aulacocyclinae in America, as well as in Africa-Madagascar, strengthen this hypothesis.

Passalidae are monophyletic. Nevertheless the hypothesis of their sister group remained unsolved. In the literature passalids were historically considered as more closely related to Lucanidae than to another family, an idea which is rather permanently maintained (ie: Crowson, 1955, 1960; Iablokoff-Khnzorian, 1977; Howden, 1982; Caveney, 1986; Scholtz, 1990; Browne and Scholtz, 1995, 1999; Hansen, 1997; Grebennikov and Scholtz, 2004; Scholtz and Grebennikov, 2005; Caterino et al., 2005; Krell, 2006; Lawrence et al., 2011; Strümpher et al., 2014). Also there is there a kind of tradition, followed by a number of more established hypothesis, but finally not demonstrated. Ultimately, molecular data support for Passalidae some affiliations with Trogidae MacLeay (Ahrens et al., 2014), and also more closely with Pleocomidae LeConte (McKenna et al., 2015). Finally, as these authors concluded, like a small consensus is still adopted for the phylogenetic relationships of some of the families of Scarabaeoidea, including Passalidae. In specific search for the sister group of Passalidae, Boucher (2006) suggested that Chironidae and Trogidae could be better placed than Lucanidae. Chironidae, a very small family, was overlooked in almost all phylogenetic studies on Scarabaeoidea. Trogidae has shown some mandibular characteristic previously only known in Passalidae, but the synapomorphies remained incomplete, and finally the required sister group was not still established. However, the present fossil from Burmese amber seems to fill this gap. Following the phylogeny of Passalidae, morpho-anatomical facts, maybe also biological presumptions, show that passalopalpids and passalids are the most closely related taxa.

We can suggest that Gondwanian passalids remained and diversified there, whereas Laurasian passalopalpids disappeared, without having reached another land. This extinction is about a certainty, and we think as a cause an unfavorable bioclimatic factor, as too temperate or too cold, or too dry, this combined with population size, allowed precise and repeated observations on the external and sometimes internal morphology. However, several specimens underwent compression and distortion, further to variable conditions of pressure and temperature of the amber since 11-12 Ma. Also fungi can block the access to details (Fig. 1). Despite this, in external sclerites only hindwings and mandibles were incompletely observed with respect to the basal part. In some specimens it was possible to determine the sex, thanks to tracks of vaginal ways or the aedeagus. However, numerous gaps still remain to give an interpretation of these initial observations.

2. Materials and methods

2.1. Origin and datation

Specimens come from inclusions in amber deposits of the Hukawng Valley, Kachin State in northern Myanmar. It is the « burmite » resin from Burma. The mining locality is at Noije Bum, near Tanai village (26°21′33.41″N—96°43′11.88″E) and is known for its spectacular richness in terrestrial Arthropods (ie: Zherikhin and Ross, 2000; Grimaldi et al., 2002; Cruickshank and Ko, 2003; Ross et al., 2010; Xia et al., 2015; Bai et al., 2016a,b). The age is estimated as ca. 99 Ma, earliest Cenomanian, following the age (98.8 ± 0.6 Ma) given by isotopic U-Pb dating of zircons from the volcaniclastic matrix of the amber (Shi et al., 2012).

2.2. Reference terminology

The followed morphological terminology, especially for the sclerites and small structures of the head capsule, mouthparts and abdomen, is that revisited or established through homologies by Boucher (2006, with index). Other terminology is basically found in Gravely (1914,1918). The terms « passaloid, lucanoid, melolonthoid, chironoid » are used in the sense of rembling or like that of members (or selected members) of the families Passalidae, Lucanidae, Melolonthidae (or Scarabaeidae Melolonthinae) and Chironidae. In many cases, these resemblances will doubtless demonstrate real phylogenetic relationships.

2.3. Measures and notification of characters

The total length of specimens is taken from the apex of elytra to the anterior border of evaginated labrum. Numbers indicated between hooks (ie: [car 23]) send back to characters used in the cladistic analysis of Passalidae by Boucher (2006).

2.4. Access to characters

The conditions of the amber, with little contamination by microparticles, the excellent conservation of insects themselves, and the used lightings, allowed precise and repeated observations on the external and sometimes internal morphology. However, several specimens underwent compression and distortion, further to variable conditions of pressure and temperature of the amber since 11-12 Ma. Also fungi can block the access to details (Fig. 1). Despite this, in external sclerites only hindwings and mandibles were incompletely observed with respect to the basal part. In some specimens it was possible to determine the sex, thanks to tracks of vaginal ways or the aedeagus. However, numerous gaps still remain to give an interpretation of these initial observations.

2.5. Observations and photos

Pieces of amber inclusions with samples were ground and polished. Several nuggets being particularly interesting, they were worked again to obtain quadrangular volumes, and to eliminate artefacts. Main observations were made with a Nachet m50 stereomicroscope 40×—120×, with powerful 250W three arms epipodiscopic cold light source; other observations with a Leica MZ 12.5. Photos were taken with a digital camera fitted to stereomicroscope, processed in Helicon Focus 5.1 software and lastly Adobe Photoshop CS6 to deal with the images. By merging several photos of the sample, at different focal planes, a single picture was created in which the entire sample was in focus.

3. Results

3.1. Systematic paleontology

Order Coleoptera Linnaeus
Superfamily Scarabaeoidea Latreille
†Passalopalpidae Boucher and Bai fam. nov.
http://www.zoobank.org/5D501119-B297-46F4-8069-9B08D608026A
Type genus: *Passalopalpus* Boucher and Bai gen. nov.

*Key characters among* Sciarabaeoidea. Habitus flat and elongated. Notum long and narrow. Dorsal structures of the head developed on the postfrontal areas. Mouthparts entirely sclerotized: mandibles large, long and powerful; labrum long, wide and spatulate; mentum trapezoid, large and flat; these characters as a whole...
passalid-like; maxillary palps very long, exceeding the outer sides of mandibles; galeae long and narrow, with strong punctuations and long setae almost everywhere, the medio-apical part like bludgeon; laciniae tridentate near the apex. Antennae with 9 articles; clubs lamellate and thick. Pronotum longer than wide. Metasternum very reduced posteriorly. Elytra striated on the five discal only and completely pubescent and like moss on sides. First legs with two rows of strong spines on each margin of ventral face and without anterior mobile spur. Procoxae very large, followed by comparable robust profemora. Metacoxae like winged, external and large. Claws with a convexity on the ventral face. Abdomen with six almost complete to complete sternites (II–VII). General pubescence heterogeneous and sometimes very long on every parts of the body and legs. Hindwings with the veins pattern of Passalidae, but with the apex very rounded.

**Detailed diagnosis.** Passalopalpidae is recognized by the following two sets of characters: passaloid characters (Passalopalpidae + Passalidae) distinguished from remaining Scarabaeoidea; passalopalpid characters, distinguished from Passalidae.

**Passaloid characters**

Habitus, body shape and head, as a whole dorsoventral, hardly distinct from a passalid (Figs. 1, 2).

Color uniform dorsoventral.

Head prognathous, quadratic, with diverse cuticular structures, such as ridges, grooves and tubercles (Fig. 3). Tentorium strongly developed.

Mouthparts (mandibles, maxillae, anterior labium and labrum; Figs. 3–4A–B) strongly sclerotized, by no means membranous or ciliated. Labial palps with narrow, long and almost hairless articles. Maxillary palps with narrow, long, distal articles. Laciniae folded, almost glabrous. Mentum trapezoid, almost plan, large, strongly concave on the medio-anterior part, where fits the ligula. Submentum completely welded with mentum. Hypostomal processes developed, flanked on both sides of the mentum and submentum. Mandibles powerful, crushing, slightly asymmetric, with 4 teeth on the incisor/molar lobes. Labrum large, quadratic, thin, spatulate, sliding under the clypeus.

Antennae typically lamellate; clubs extended on one side, into thick articles (Fig. 3); antennae very mobile, they can wind under the cephalic capsule; either articles deploy completely forward, almost straight, as observed on some specimens. Scape bend and clearly longer than other articles. Clubs more or less completely froth except bottom, very distinct from other articles, which are smooth.

Notum elongated, exposed dorsally, separating widely the pronotum from the elytra (Figs. 2, 5).
Elytra clearly striated (Figs. 1A, 2A).
Tarsi pentamere (Figs. 5, 6D).
Meso- and metatibiae rather long and narrow, with two terminal mobile spines (spolons; one ventral and one dorsal) and two fixed spines (one ventral and one dorsal), more the terminal fork (Figs. 6D–F).
Abdomen with sternites II–VII complete or almost complete; I vestigial (Fig. 5, I not shown).

Passalopalpid characters

These characters do not exist at any Passalidae.

Habitus clearly widened on elytra (Figs. 1–2).
Pubescence on the head, pronotum, elytra, abdomen, legs including tarsi, of conformation (thickness and form) and length, very composite. Numerous very long setae are either scattered (elytra, abdomen), or in dense tufts (head), or regularly arranged (profemora, protibiae). Presence of dorocephalic pubescence, laterofrontal, mediopostfrontal and supra-ocular, very long and in dense tufts. Pubescence on side of elytra dense everywhere and diversified, as well as on the anterior border and on the humeral calli. Pronotum: anterior border without pubescence like short brush, but with some long and spaced setae. Legs: setae not more in brush on outer margin of tarsal pit, but as on side of elytra, although less numerous (Figs. 5–6).

Head capsule: basis, near the foramen magnum, narrow (not widened) and regularly rounded (Fig. 3A). Dorsal cuticular structures (ridges and tubercles) only related to supra-ocular ridges and/or to epicranial sutures (Fig. 3).
Antennae with 9 articles. Clubs with numerous and very small, but prominent, setae, especially on distal articles VIII–IX (Fig. 3).
Mandibles thin and sharp, but with four powerful, conical and almost regular teeth, arranged on the same plan; only one apical tooth and three internal teeth; infrabasal pits long and subparallel (Figs. 3–4).
Maxillae: maxillary palps with two long and narrow distal articles, exceeding many the outer sides of mandibles; galeae (outer lobes) long and narrow, covered with strong punctuations and long setae almost everywhere, including near the medio-apical part like bludgeon; laciniae (inner lobes), with on the internal margin three sharp distal spines and a stronger postmedian spine (compared with Passalidae, Fig. 4).
Ligula reduced towards the mentum (Fig. 4A).
Hypostomal processes welded, on almost all their length, with the head capsule (Fig. 4A).

Pronotum rectangular, thin, longer than wide. Dorsolateral: integument more or less micro-punctured and wrinkled; median groove very wide in the middle; no margino-anterior nor lateral grooves; lateral pits very large, covering almost the length of the sclerite; lateroposterior margin concave. Ventral: anterior border with two strong lateral cavities (Figs. 1, 2, 5).

Mesothorax, as a whole, dorsally finely setigerous (Figs. 2, 5).
Metasternum with lateroposterior areas extremely reduced close to coxae (Fig. 5).
Procoxae very large, oval (Fig. 5).
Profemora very short, very wide on the basis, almost triangular (Figs. 1B, 5).
Protibiae curved, with two ventral rows of strong spines; no apical spolon; tarsal pit with the outer margin slanted; dorsolateral setae of two types: very long and spaced, or short, numerous and scattered (Figs. 6A–C).
Mesotrochanters narrow and elongated (Fig. 5).
Meso- and metatibiae with the superior spolon very long and the apex slightly spatulate (Figs. 6D–F).
Metacoxae like winged, external and very large (Fig. 5).
Elytra thin, clearly widened on the postmedian part; integument micro-granulous and without lateral striae; 5 discal, little marked, striae and interstriae; apex strongly concave and rounded; anterior border concave and sharp (Figs. 1A, 2A).
Hindwings with the apex very rounded, although macropterous; sometimes one supplementary infra-costal vein instead of median fold (Fig. 7A).
Tarsi elongated and oval; claws convex on their inferior margin (Figs. 6D–E).
Abdomen: sternites II–VII complete, the first one a little shrunk in the middle; II–III with a marked pit close to metatrochanter; II–V with a small lateral pit. Mediotergite VIII exposed dorsoventral, exceeding the abdomen (Figs. 1B, 5, 7B).

Etymology. Given the systematic interpretation of the taxon and its so peculiar maxillae.

Fig. 2. Passalopalpidae fam. nov., Passalopalpus cheni gen. et sp. nov. Habitus of the head, pronotum and elytra. A. dorsal. B. lateral, pubescence of laterofrontal and postfrontal areas, mandible and gena, not shown. Scale: 1 mm.
**Passalopalpus Boucher and Bai gen. nov.**
http://www.zoobank.org/C9938F35-7472-46AB-9F34-A921CC0250A3
Type species: *Passalopalpus cheni* Boucher, Bai and Zhang sp. nov.

**Diagnosis.** By monotypy in the family, characters of the genus relate to those established previously.

**Passalopalpus cheni Boucher, Bai and Zhang sp. nov.** (Figs. 1e7)
http://www.zoobank.org/74659848-C34D-424D-B04C-D5D047C8EB0E

Type material: 27 specimens from 24 pieces of amber from Hukawng Valley (see above). — Holotype, male, No NIGP163563, and eight paratypes No NIGP163564, NIGP163560 (with two specimens), NIGP163561, NIGP163562, NIGP163565, NIGP163566, NIGP163567 and NIGP163568, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. — Five paratypes, No BU-001782, BU-001897, BU-002077, BU-002119 and BU-002207, currently on long-term loan in the Institute of Zoology, Chinese Academy of Sciences (IZAS) (specimen available for study by contacting MB or WWZ). From 2026 these five paratypes will be deposited in the established Three Gorges Entomological Museum, Chongqing, China. — Ten paratypes on loan to SB, No PASP1 (with two specimens) to PASP10 (three of them deposited in the MNHN). — Two paratypes (in one piece) on loan from coll. Anders Damgaard (Denmark).

**Description.** Macropterous. Habitus depressed, widely pubescent, elongated and narrow, except widened elytra (Figs. 1A, 2A). Color of body and legs light brown ventral and dorsal (Fig. 1).

**Dimensions** very small for a passaloid species. Total length: 7.4–7.6 mm; greatest width: 1.3–1.4 mm over elytra; smallest width: 1.7 mm over pronotum; thickness: 0.4 mm.

**Head** (Fig. 3). Frontal border, on half concave, thin and with some setae more or less long and spaced; sides prominent, clearly more sclerotized than elsewhere; external angles powerful and thick, apex curved and thorny upward, forming anterior angles of head. Clypeus exposed, thin and hyaline, short and transverse, a little wider than the labrum, which it recovers on base. Labrum large, narrower on base, anterior border convex. Medio- and laterofrontal areas large, concave, deep and without any cuticular structure (ridge or tubercle); integument smooth or almost; anterior mediofrontal area glabrous; laterofrontal areas, anteriorly with long and scattered setae, posteriorly with a tuft of very long and dense setae close to supra-ocular ridges. Posterior mediofrontal area concave as previously, but forming a narrow cavity with a dense tuft of setae, most of them very long, of uneven lengths and sometimes thickness. Epicranial sutures not revealed (see below, Section 4). Lateropostfrontal areas convex; integument smooth, with setae in tufts less dense and less long than previously. Postfrontal groove transverse, marked, waved, interrupted in middle by cavity of posterior mediofrontal area, and reaching almost inner sides of supra-ocular ridges. Postfrontal area glabrous, with light anteroposterior lines on almost all width. Supra-ocular ridges strong, high and thick, separated from angles of head by a rather clear cavity, then 1) behind forming a short oblique edge with a small tubercle in every extremity, then 2) a long and straight anteroposterior edge reaching postfrontal groove, then 3) a low edge, curving behind eye. Latero-ocular pit large and deep,
connecting eye and supra-ocular ridge, with numerous short to very long setae. Eyes very close to passalids, almost globulous, exceeding head width. Ocular canthus rather short and narrow; apex obtuse shorter than eye. Postocular pits obsolete, or gobbled up into latero-ocular pits, with small and scattered setae. Antennae with 9 articles, rather long; scape long and curved; scape and articles II–VI smooth, with 2–3 setae each; clubs with 3 rather long articles, thick, convex down, with numerous minute but prominent setae, more on VIII and IX. Mandibles (Figs. 3, 4A) powerful and regularly waisted, but thin. Dorsal face hairless and smooth except on basal part, with a tuft of short setae and punctuations; inner lobes with 4 strong teeth, conical, on same plan with comparable development and conformation; dorsal teeth double, on a high ridge; distal tooth almost acute, exceeding outer margin of mandible (similar to lateromandibular tooth of some Passalidae, but not homologous; see Boucher, 2006); proximal tooth higher and longer. Ventral with a long pit, parallel to outer margin (Fig. 4A), Ligula (Fig. 4B) small, covered with setae; labial cavities large; anterior border a little convex. Labial palps (Fig. 4A) with 3 developed articles, straight, smooth and with rare setae. Maxillae (Figs. 4A–B) with long and straight maxillary palps of 4 articles, exceeding half their length the lateral edges of mandibles, smooth except some rare proximal setae; galea very developed, long and straight, widened before apex, with numerous, strong and long setae almost everywhere; lacinia folded, smooth and hairless or almost, with three inner distal spines, strong, sharpened and of uneven lengths, more one strong and wide inferior spine. Mentum (Fig. 4A) large, trapezoid; disk somewhat convex; winged sides with outer margin slightly curved upward; no lateral pits; integument almost smooth, except very short and spaced setae. Submentum (Fig. 4A) large, convex on sides, with numerous punctuations and rather long setae almost everywhere. Hypostomal processes wide and long (Fig. 4A), flanked laterally, completely welded in the submentum, hairless and smooth, with a large central pit. Pronotum (Figs. 1–2, 5) thin, narrow and elongated, 1.5 longer than wide. Dorsal: anterior border weakly concave; anterior angles well rounded; sides slightly concave on half of median length; marginal
VIII. Scale: 1 mm.

Little deep and wide, more or less parallel; interstriae smooth or marked, reaching almost posterior border of pronotum, but not punctuated. Setae of very uneven lengths and thicknesses, set presenting a silky aspect very distinct from the hairless disk. Apex rounded, thin, very concave at junction of elytra, where mediotergite VIII is clearly exposed dorsally. Hindwings (Fig. 7A) of macropterous type, hyaline and clear, exceeding (displayed) by 1/5 the length of elytra. Anterior fold marked by a clear apophysis on the thick and long costal vein. Radial and median veins I–II developed. Sometimes one supplementary infracostal vein instead of the median fold of Passalidae. Basal part of the wing not accessible to the observation on our samples.

Coxae (Fig. 5). Procoxal fosse very large and oval. Mesocoxal pit small and oval. Metacoxae external, very large, movable and like winged, covering sternites II–III, and with scattered long setae; metacoxal pit extremely reduced.

Legs long and rather slender, setigerous. Profemora (Fig. 5) are an exception, as short and very wide on the base; margino-anterior setae rather short and numerous; margino-posterior setae extremely long and regularly spaced out; ventral medio-apical setae short and grouped. Mesofemora (Fig. 5) narrow and elongated, sub-parallel; margino-anterior setae rather long, scattered and numerous; margino-posterior setae longer and spaced out. Metatibiae (Fig. 5) of intermediate conformation with the previous, rather thickset; setae as in mesofemora, but reaching the mediodistal area. Protibiae (Figs. 5, 6A–C) very narrow; outer face slightly concave; ventral face armed with two rows of spines, each row with 5–6 more or less strong spines, sometimes sharpened and of uneven lengths, more apical fork, powerful and strongly curved downward; dorsal crest little marked, with 9–10 long scattered setae; inner face with fine and dense setae like brush, more some distal setae; outer face with scattered setae of uneven lengths; tarsal pit long, with not thorny and very slanted margin, and without spolion. Mesotibiae (Figs. 5, 6D) somewhat widen, with 3–4 median or postmedian spines, the first one and the last one stronger than the others; dorsal setae rather numerous, of very uneven lengths, a series of 5–6 being extremely long and more thick; setae of ventral and inner faces scattered and of uneven lengths; apical forks wide and sharp; superior spolion very long, straight, apex almost spatulate; inferior spolion long, almost straight, sharp. Metatibiae (Figs. 5, 6F) finer and longer than mesotibiae, inermous; upper crest obsolete; setae more numerous; apical forks and spolions as in mesotibiae. Tarsomeres (Figs. 6F) with 5 articles; I–IV face, elongated and beveled/pointed, with 2–3 main apical setae on the lower and upper faces, more some scattered shorter setae; claws (Figs. 6E–F) long, thin and strongly hooked, thickened on the lower face, with a pair of mediofrontal short setae and a double pair of long basal setae.

Abdomen (Figs. 1B, 5) long and wide, but thin. Ventral; integument more or less smooth, without transverse sours, except on epimeria with numerous setae of uneven lengths and thicknesses, certain very long; 7 visible sternites; complete II–VII, but II with a small shrunken in the middle; I invaginated except on sides; II–III with two clear paramedian notches (where comes to find accommodation trochanters in movement), however these sternites poorly visible when abdomen in normal position under the metathorax; II–V with a small elongated concavity on each side; outer border of VII rounded, without groove (Fig. 7B). Dorsal: mediotergite VIII exposed, exceeding the apex of elytra and with plentiful short or long setae (Fig. 2A dorsal; 5 ventral). Adeagus not clearly visible on samples. We distinguish only, on two specimens, a part of the phallic, apparently a little bit spherical.


Fig. 5. Passalopalpidae fam. nov., Passalopalpus cheni gen. et sp. nov. Thorax and abdomen (ventral). Thorax slightly dislocated; pubescence of prothorax partially shown; empty coxal cavities in gray; S II–VII: sternites II–VII; Mtg VIII: mediotergite VIII. Scale: 1 mm.
3.2. Observed characters and preliminary phylogenetic interpretation

The family Passalidae was formally recognized monophyletic on the basis of a cladistic analysis of 38 morpho-anatomical characters. Argued extra groups were the genera Sinodendron Schneider (considered amongst primitive Lucanidae), Trox Fabricius (Trogi-
dae) and Theotimus Huchet (Chironidae). The monophyly of Passa-
ilidae was strengthened by 8 not ambiguous characters from sclerites of the body and appendages: [car. 3] number of teeth of the incisor apex of mandibles; [car. 9] development of hypostomal processes; [car. 13] development and position of the ligula; [car. 14] development of the mentum; [car. 25] development of the medi-
opostfrontal structure (central and lateroposterior tubercles); [car. 26] development of the lateropostfrontal area; [car. 34] conformation of the notum/scutellum; [car. 35] development of legs III of the larva (details in Boucher, 2006).

Fig. 6. Passalopalpidae fam. nov., Passalopalpus cheni gen. et sp. nov. Legs. A–C. Protibia (D: right dorsal; L: lateral; V: ventral ¼ external, with first tarsomere). Pubescence not shown in ventral. D. Mesotibia (right dorsal). E. Metatibia claw (frontal). F. Metatibia (right dorsal) with tarsi (lateral). Scale: 0.5 mm.

Two of the 38 characters from this analysis were unavailable for observation on passalopalpids: the basal « appendage » of the right mandible [car. 6] and posterior legs of the larva [car. 35]. Consequently, 36 character states of Passalidae remain informative in passalopalpids.

Possible sister groups: « not ambiguous » character states in Passalidae + Passalopalpidae

Six (8 less 2, see above) not ambiguous character states during the reference analysis of Passalidae, only the two following are distinct in Passalopalpidae:

- the most apical tooth of the incisor lobe, or apex of mandibles [car. 3] is occupied by the supraterminal tooth (Figs. 3–4A). In passalids the apex is always occupied by the mediointernal tooth of same incisor lobe. Moreover or consequently, in pas-
alopalpids the complete incisor lobe (supra-terminal + mediointernal + infraterminal teeth) is on the same horizontal plan than the distal molar lobe (supra-internal + infra-internal teeth) (Figs. 3–4A). In passalids the two lobes are always on two distinct plans, thus mandibules are curved.
These two different architectures for a homologous set of mandibular structures is an essential evolutionary process in each group.

- the mediopostfrontal structure [car. 25] of Passalopalpidae has, instead of the convexities of Passalidae (mainly central and lateroposterior tubercles), a vast cavity on all the area between the supra-ocular ridges (Fig. 3). Besides, the development of the supra-ocular ridges, which are very high in Passalopalpidae, exists as such at no Passalidae.

It is the most likely that the four remaining not ambiguous character states found in Passalidae and Passalopalpidae are homologous and plesiomorphic.

Character states shared only by Passalopalpidae and extra groups

From the 36 informative character states, only that of the tridentate lacinia is shared with an extra group, formally Trox [car. 12]. This can be a homology as well as a convergence. It is an exception which strengthens the phylogenetic affinity of Passalopalpidae with Passalidae.

Character states shared by Passalopalpidae and Passalidae Aulacocyclinae

They are many, with 14 of the 36 informative character states. Nevertheless, this interesting fact does not obviously question the membership of the subfamily Aulacocyclinae in Passalidae; [car 2] the three teeth of the incisor lobe (supraternal + medioterminal + infraterminal teeth) are on the same horizontal plan, this state existing however in two of the tribes of Passalinae (clade Passalini + Proculini); [car 5] absence of mobile infra-internal teeth of the distal molar lobes; [car 6] absence of the right basal mandibular « appendage »; [car 7] absence of extrabasal teeth, this state also being in Passalinae, Passalini + Proculini; [car 16] three articles on the antennal clubs, this state also being in Passalinae, except Macrolinini; [car 18, 19] absence of lateroclypeal pits; [car 20, 21, 22, 24] absence of laterofrontal tubercles, secondary laterofrontal tubercles, secondary mediofrontal tubercles.
and anterior and posterior frontal ridges; [car. 28] absence of lateroposterior tubercles; [car. 29] absence of epicranial pits; [car. 33] anteropronotal groove incomplete (details in Boucher, 2006).

We shall note the supra-ocular ridges which are strong to very strong in Passalopalpidae [car. 31], but the homology of this character state with the Passalidae Aulacocyclinae remains very uncertain. Indeed, these ridges have a distinct conformation in both groups. It can involve a convergence.

Besides, no character state is only shared by Passalopalpidae and Aulacocyclinae. This information accentuates the position more "derived" of the Aulacocyclinae (or more basal of the Passalinae) within Passalidae, as well as the basal dichotomy of both sub-families, as suggested by Boucher (2006).

**Character states shared only by Passalopalpidae and Passalidae Passalinae**

They count 5 of the 36 informative characters: [car. 1] habitus, dorusventral, ellipsoid; [car. 10] sides of hypostomal processes horizontal; [car. 30] anterior angles of the head formed by the angles of the epicranium; [car. 32] development of the sternum half way up coxal projections; [car. 38] six visible sternites. None of these states belongs to the previous not ambiguous characters.

**Character states not shared by Passalopalpidae and Passalidae Passalinae**

They are many: 11 of the 36 informative characters: [car. 3] apex of the mandibular incisor lobe is simple; [car. 5] absence of mobile infra-internal tooth of the distal molar lobe; [car. 6] absence of the right basal mandibular « appendage »; [car. 12] apex of lacinia tridentate; [car. 18] absence of lateroclypeal pits; [car. 20] absence of laterofrontal tubercles; [car. 23] absence of anterofrontal ridges; [car. 25] no development of the medioposterfrontal structure (mainly central and lateroposterior tubercles); [car. 28] absence of lateroposterior tubercles; [car. 29] absence of epicranial pits; [car. 33] anteropronatal groove incomplete. This general distribution of character states underlines the former dichotomy between presumably sister groups, Passalopalpidae and Passalidae.

### 3.3. Polymorphism, sexual dimorphism

Polymorphism is poorly marked for the body size and all remaining characters. As in Passalidae, the development of dorsocephalic structures is somewhat variable, such as the frontal border and the supra-ocular ridges. On the other hand, the setae types, so numerous, their length, abundance and distribution on the head and the rest of the body, are very stable amongst the examined specimens.

It was possible to distinguish the sexes on some specimens, thanks to the partially evaginated genital structures. However, an external sexual dimorphism was not found. In passalids, the sexual dimorphism is very rare, and it is known only in a few Passalinae, genera *Leptaulax* Kaup (Leptaulacinia in Asia) and *Paxillus* Mac Leay (Passalini in America). Otherwise, females are generally a little bigger/longer than males, without it is a strict rule.

### 4. Discussion

#### 4.1. General morphology

The general morphology of the passalopalppid species is remarkable on various points. Some major characters are fully comparable to passalids, and most underline the narrow affinities of both families. Some relevant characters and other preliminary remarks deserve to be noticed.

**Maxillae.** Amongst mouthparts, maxillae look like « Hexapalps », by analogy with some groups of Adephaga, Caraboidea, named as such, between the 19th and 20th Centuries (ie: Houlbert, 1912, 1920; Göldi, 1912; Bertrand, 1954; Séguy, 1967). In this peculiar scheme, the galea resembles a biarticulate palp, and the whole maxilla seems constituted by three palps: maxillary palp, palpiform galea and labial palp, x 2, or « hexapalps ». Also in the passalopalpid, maxillary palps are very long and exposed in dorsal view of the insect; they exceed widely, permanently, on each outer side of the mandibles (Figs. 1–4).

This reminds again many Caraboidea. Which is absent in all passalids. This morphology seems to show an evolutionary process described by morphologists in Coleoptera and in other insects: the progressive transformation and division of the maxilla (ie: Snodgrass, 1935; Matsuda, 1965; Denis and Bitch, 1973; Chaudonneret, 1990; also useful data in Nel and Scholtz, 1990; Labandeira, 1997). Basically in Scarabaeoidea, the plesiomorphic external lobe, or galea, is somewhat membranous, and certainly sensorial, whereas the internal lobe, or lacinia, is more or less denticulate and like folded. In this way, the galea of passalopalpids is like a supplementary classical palp, with long setae, and only the lacinia is folded. In Passalidae the lacinia and the galea are both strongly sclerotized, folded, almost smooth, and to the best of our knowledge, not sensorial. What does not confer any more to the galea the aspect of a true « palp. Thus, the transition between passalopalpids and passalids could show an evolutionary process within the passaloid lineage, and to which no other group of Scarabaeoidea seems to correspond.

**Mandibles.** They are much simple, on various points more rudimentary than Passalidae. We find there some possible basal characteristics of passaloid, in particular the number of 4 teeth of the incisor/molar lobe, thus as in Passalidae. However, the arrangement of the teeth is very different in both families. The rudimentary state underlines a set of plesiomorphies in the passalopalpid.

Further study is necessary to know the conformation of some hypothetical or not observed structures in passalopalpids: the most basal tooth of the distal molar lobe (infra-internal tooth), the molar table of the proximal molar lobe, and finally the right basal « appendage », such as we find in passalids.

**Dorsocephalic small cuticular structures, mainly tubercles and ridges.** These small structures, essential in the basal scheme of the head and in the systematics of passalids, as interpreted by Boucher (2006), are absent in the passalopalpid. The fossil has indeed apparently no character of this scheme from passalids such as: central tubercle + lateroposterior tubercles → posterofrontal ridges → inner tubercles → anterofrontal ridges → frontal tubercles.

The only clear structures on the dorsal face of the head in the passalopalpid are the high ridges which follow, apparently (exactly ?), the running of the epicranial sutures (Fig. 3). It is surprising that no track of comparable sutures was formally observed close to these ridges. So that we could think that the ridges — here identified as supra-ocular ridges — would correspond themselves to the epicranial sutures. In this condition the supra-ocular ridges would not then be homologous in passalopalpids and passalids. One of the two hypotheses will have to be demonstrated.

**Pronotum.** The shape (long and narrow) and the median groove (very widened) of the pronotum (Fig. 2) look like a lycanoid of the small species of Lucanidae, Figulinae, but at no means passalids.

**Anterior border of elytra.** The clear concavity and sharpness of this part of the sclerite (Fig. 2) are absent in passalids and seem to be more closely related to lycanoids. This character state exists in many groups of Lucanidae and other Scarabaeoidea.

**Antennae.** With 9 articles (Fig. 3), instead 10 in all passalids, antennae are thus very distinct. In details each article is much more angular than in passalids.

**Metacoxae.** Being not invaginated, but external, somewhat movable and developed as a flat plate (Fig. 5), they are extremely...
different from passalids and are plesiomorphic. In passalopalpids, when the coxae are in normal position, and when the abdomen is normally contracted, only the sternites IV–VII remain clearly exposed. On the other hand, when the metacoxae are moved upward and the abdomen somewhat dislocated, then the abdomen is entirely exposed, showing the almost complete sternite II and complete sternite III.

**Abdomen.** The 5 complete sternites III–VII + 1 sternite a little reduced close to coxae (II), more the exposure of the mediopterite VIII (Figs. 2A, 5), are plesiomorphic character states. In Passalidae only the sternites IV–VII are complete, whereas the mediopterite VIII is not visible in ventral view as it is almost vertical. Besides, the small, but marked, paramedian notches on sternites II–III in passalopalpids are probably showing the evolution of the sclerites in other passaloids: in Passalidae Passalinae the II disappeared almost, or disappeared completely in Aulacocyclinae, whereas the III is in an advanced process of reduction close to coxae, in both subfamilies (details in Boucher, 2006). The sternite I is also visible in the passalopalpids, when the metacoxae are moved upward, as two small triangular and very lateral sclerites; in Passalidae a similar conformation exists, but with the sternite II only.

**Tibiae.** One of the most surprising characters of the ambulatory appendages of passalopalpids, before the pubescence and claws, is the absence of mobile spine (also called spolon or mobile spur) on the distal part of protibiae (Fig. 6A), contrary to all passalids. It is here also about a plesiomorphic character state. The two ventral rows of spines of protibiae are also very distinct from passalids (with only one outer row of spines).

**Profemora.** As such in passalopalpids, so wide and short (Fig. 5), they do not exist in any passalid (including some Aulacocyclinae, in spite of some appearances), but are of chironoid conformation.

**Tarsomeresh.** Their general aspect is close to many lycanoids. In passalids the inferior apex of each article is never slender as such, but more or less slightly beveled and rounded.

**Claws.** The claw of each pretarsus, which has a permanent pair of small inferior convexities (Figs. 6E–F), seems to be melolonthoid, but not related to passalids (without any convexity).

**Pubescence.** As for claws, the general pubescence of passalopalpids (Figs. 2–3, 6–7B) is not related to passalids, but to melolonthoid. Also, the short setae like comb, symmetrical and that we find in all passalids at the base of the protibial pits, on the anterior and posterior margins of the pronotum, on the anterior margin of the frons or clypeus, as well as on the crest of tibiae, exist by no means in passalopalpids. On the contrary, in this last taxon the setae are very ill-assorted in their conformation, arrangement and abundance; this state can be only plesiomorphic.

### 4.2. Possible relationships between body color, body size and distribution pattern

The color of the body and the legs of Passalidae is known for its extreme uniformity (as in Chironiidae, but otherwise a group very poorly diversified, and also in Trogidae). Almost all passalids are entirely black shining. Subtle variants exist however, going to blue-gray, more or less opalescent to matt. A clear distinction is noticed between many species and from various species groups. Also exist a few bicolored species, thanks to a process of durability of a segmented part of the brown-red immature stage integument. These species belong only to the genus *Leptaulax* (Passalinae, Leptaulacini), from South-East Asia and Melanesia. Finally, some other species keep permanently their whole brown immature color, in diverse degrees. It is the case, in the Passalinae only, in the African genus *Didimus* Kaup, such as *D. elaienesis* Hincks (Solenocyclini), in the American genus *Spasalus* Kaup (Passalini), the two sister species *S. kaupi* Boucher and *S. seag* Boucher, or in various species of *Leptaulax*. All examined passalopalpids are also brown, by considering that the observed pigmentation is the one of origin and that of mature stages.

A second comparison to be made between the mentioned passalid species is their very small body size, compared to the other species of the family. They do not exceed 13–15 mm or hardly. Passalopalpids do not exceed 7.6 mm (Xia et al., 2015, cited 7–9 mm, what seems doubtful beyond 8 mm for *P. cheni*).

A third comparison to be made between the same species of Passalidae *Spasalus, Didimus* and *Leptaulax* is their endemism. They live amongst some of the oldest and largest rain forests of the World: the margins of the Amazonian Basin, the upper Basin of Congo, and Borneo in the Great Sunda Islands. The distribution of these peculiar species on different continents maybe are to be related with the previous presumably plesiomorphic character states, color and body size. It is conceivable that oldest passaloids were very small, with brown integument, and that they were distributed in tropical wet forests. Some characteristics which could be comparable to the passalopalpid species.

### 4.3. Biology

**Fly ability.** The morphology of the hindwing of passalopalpids is close to that of Passalidae. We find in passalopalpids a ratio near 1 between the lengths of the body and the wing, which corresponds to the current ratio for macropterism and fly ability in Passalidae, as shown for example in the large American genus of Proculini, *Veturius* Kaup (Boucher, 2006). Consequently, it is the most likely that passalopalpids could fly, easily.

**Food and microhabitat.** To date it was not possible to study residual contents from the alimentary canal of passalopalpids. However, resin also contains many detritus and other organic particles, almost in contact with passalopalpids. A large part of these detritus seems to be like structures from ligneous plants. It is thus likely that passalopalpids were associated with decayed big plants or trees. Except rare instances, Passalidae are confidently dependent on dead wood. This relation, or not, must be more examined with regard to the passalopalpids.

**Behavior.** Passalids are one of the rare families of subsocial beetles (see overview in Castillo and Reyes-Castillo, 2008). Larvae and adults live in family groups and coexist necessarily. In all species is established a social structure within a system of galleries which they dig in rotten wood. Larvae and adults communicate in particular by sounds that they produce and receive. This uniform biology is thus plesiomorphic for the family, whereas isolated specimens cannot survive for a long time. In the Burmese amber, the presence of several specimens of passalopalpids in the same nugget of resin, as well as so numerous specimens in the same deposit, allows to think that these insects were gregarious at least. However, at the moment the study of hindwings and elytra did not reveal any stridulatory apparatus, such as it is known in all Passalidae.

### 5. Conclusion

Further to the observations and descriptions of Cockerell (ie: 1917, 1922), numerous fossils of Arthropods were discovered in the earliest Cenomanian amber of Burma. Passalopalpids represent the first known passaloid beetle of the Cretaceous. They are much older than the fossil rocks of Passalidae known up to now and are very different from them. Consequently, these two kind of fossils did not belong to comparable faunas. However, both families belong undoubtedly to the same lineage. It seems that passalopalpids are not rare in the Burmese amber and they form a source of invaluable informations. This initial study accentuates phylogenetic and
paleobiogeographic considerations and contribute also to the knowledge of Passalidae. We think that other species of passalo-
palpids will be discovered and that they will come to complete and strengthen the observations and interpretations. Other available data will be studied on the passalopalpids of the Burmese amber; in particular with a detailed phylogenetic analysis, on their biology and on their natural environment.

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References

Westwood, J.O., 1834. Description generum nonnullorum novorum et familiae Lucen