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MORPHOLOGICAL AND MACROEVOLUTIONARY ANALYSIS OF TARSAL CLAWS IN CRAB SPIDERS (THOMISIDAE)

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"Seen in the light of evolution, biology is, perhaps, intellectually the most satisfying and inspiring science. Without that light it becomes a pile of sundry facts - some of them interesting or curious but making no meaningful picture as a whole"

Theodosius Dobzhansky

Dedico este trabalho a minha mãe Margareth Massim Marques, meu pai Jairo César de Oliveira Marques, minha irmã Jamyle Massim Marques e a minha avó, Vilma dos Santos Massim, cujo apoio, não só nesta, mas em todas as etapas da minha vida acadêmica, foi de extrema importância. Amo muito vocês. Obrigado!

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SUMÁRIO

RESUMO

As garras são importantes estruturas na vida dos artrópodes, auxiliando não apenas na fixação, mas também na captura de alimento, no comportamento de cópula e na manipulação de materiais para a construção de abrigos ou armadilhas. Em aranhas, um grupo polifilético conhecido como Dionycha é caracterizado por possuir somente duas garras tarsais (ou uma terceira, extremamente reduzida) e cerdas para adesão a superfícies lisas. Dentro deste grupo encontra-se Thomisidae, a sétima maior família de aranhas do mundo, cujas espécies são caçadoras de emboscada que possuem especializações para captura de presas em suas pernas dianteiras (I e II) e forrageiam, em sua maioria, sobre partes aéreas em plantas. Muitas espécies em Thomisidae apresentam redução ou ausência destas cerdas adesivas, sugerindo que a garra exerce o papel principal na fixação destes animais no substrato. O objetivo deste estudo foi comparar a morfologia das garras entre espécies em um contexto evolutivo, testar a existência de dimorfismo sexual, avaliar a morfologia das garras entre diferentes pernas, verificar a existência de sinal filogenético na morfologia das garras e testar sua correlação com o substrato de forrageiro das espécies. Nossos resultados sugerem que a morfologia das garras varia apenas a nível de genérico, com gêneros próximos também mantendo diversas características em comum. Como esperado, devido ao alto dimorfismo sexual na maioria das espécies de Thomisidae, o dimorfismo sexual foi detectado nas garras de todos os gêneros analisados. Em geral, a morfologia das garras corresponde ao padrão descrito para as pernas na literatura para maioria das espécies de Thomisidae: membros anteriores (I e II) proporcionalmente maiores que os membros posteriores (III e IV). As garras dos membros anteriores são maiores e menos curvas que as garras dos membros posteriores. Diferente do esperado, apenas garras mesiais das pernas I e II apresentaram sinal filogenético maior que o esperado ao acaso; um resultado ambíguo, uma vez que a maioria das espécies e gêneros filogeneticamente próximos não apresentaram diferença significativa na comparação da morfologia das garras. A correlação com substrato foi relatada para garra ectal da perna I e para as garras mesias das pernas II, III e IV. Contudo, estes resultados parecem não corresponder a um padrão biológico existente, e, considerando que espécies com formas diferentes de garras podem forragear no mesmo substrato, concluímos que a forma das garras não está correlacionada com o substrato forrageiro por si só.

Palavras-chaves: Evolução; Morfometria geométrica; Morfologia comparada; Métodos comparativos filogenéticos.

ABSTRACT

Claws are important structures in the life of arthropods, helping not only in attachment, but also in food capture, copulation behavior and handling materials for the construction of shelters or traps. In spiders, a polyphyletic group known as Dionycha is characterized by having only two tarsal claws (or a third, extremely reduced) and setae to adhere on smooth surfaces. Within this group is Thomisidae, the seventh largest family of spiders in the world, whose species are ambush hunters who have specialization for capturing prey on their front legs (I and II) and forage, mostly, on aerial parts in plants. Several Thomisidae species show a reduction or absence of these adhesive setae, suggesting that the claw plays the main role in fixing these animals to the substrate. The objective of this study was to compare the morphology of the claws between species in an evolutionary context, to test the existence of sexual dimorphism, to evaluate the morphology of the claws among different legs, to verify the existence of a phylogenetic signal in the morphology of the claws and to test its correlation with the forage substrate of the species. Our results suggest that the morphology of the claws vary only at genus level, with close genera also maintaining several characteristics in common. As expected, due to the high sexual dimorphism in most Thomisidae species, sexual dimorphism was detected in the claws of all analyzed genera. In general, the morphology of the claws corresponds to the pattern described for the legs in the literature for most Thomisidae species: forelimbs (I and II) proportionally larger than the hindlimbs (III and IV). The claws of the forelimbs are larger and less curved than the claws of the hindlimbs. Different from expected, only mesial claws of legs I and II showed a phylogenetic signal greater than that expected at random; an ambiguous result, once most phylogenetically close species and genera did not show significant difference when comparing the claw morphology. Correlation with substrate has been reported for ectal claw of leg I and for mesial claws of legs II, III and IV. However, these results do not seem to correspond to an existing biological pattern, and, considering that species with different claw shapes can forage on the same substrate, we conclude that the claw shape is not correlated with the foraging substrate by itself.

Keywords: Evolution; Geometric morphometric; Comparative morphology; Phylogenetic Comparative Methods.

APRESENTAÇÃO

As garras são estruturas localizadas na ponta do tarso de artrópodes, responsáveis por muitas das interações destes organismos com seu habitat (Barrows, 1925; Labarque et al., 2017). Elas facilitam a locomoção, dão suporte ao animal, promovem adesão ao substrato ou hospedeiro, permitem capturar e manipular o alimento, facilitam o comportamento de cópula, carregamento da prole e manipulação da seda para construção da teia (Schultz, 1989; Dunlop, 2002; van der Ham et al., 2008; Wolff et al., 2015). Devido a esta diversidade funcional, há muitas informações morfológicas que podem ser úteis à reconstrução filogenética e aos estudos evolutivos e ecológicos nesta estrutura (Schultz, 1989).

Em aranhas os apêndices locomotores são divididos em sete podomeros articulados, nomeados do sentido proximal para o distal respectivamente de: coxa, trocanter; fêmur; patela; tíbia; metatarso; e tarso — Fig. 1(A) — (Barrows, 1925). Este último, sustenta duas garras superiores, projetadas em uma fina membrana cuticular flexível, podendo apresentar uma série de projeções ventrais chamadas de dentes — Fig. 1(B) — (Barrows, 1925; Labarque et al., 2017). Uma terceira garra localizada abaixo e entre as garras superiores também pode ser encontrada no tarso, sendo responsável pela manipulação da seda na construção da teia (Shultz, 1989). Algumas famílias de aranhas apresentam redução ou ausência desta terceira garra, e são conhecidas como Dionycha.

Dionycha é um grupo polifilético que compreende cerca de 17 famílias de aranhas, agrupadas com base na presença de somente duas garras tarsais (Petrunkevitch, 1928) e cerdas de adesão a superfícies (Ramírez, 2014). Dentro deste grupo encontra-se Thomisidae, a sétima maior família de aranhas do mundo, conhecidas popularmente como aranhas caranguejo, incluindo 2625 espécies e 170 gêneros (World Spider Catalog 2020).

Aranhas caranguejo são predadores de emboscada que não constroem teias para caçar (Morse, 1985). Seus pares de pernas anteriores (I e II) são proporcionalmente avantajados e apresentam especializações para a captura de presas, tais como: protuberâncias femorais e espinhos na tíbia e metatarso (Morse, 1985). Elas estão intimamente ligadas a seus substratos de caça, com algumas espécies forrageando sobre folhas e flores, utilizando contraste UV chamativo à visão de suas presas e outras sobre

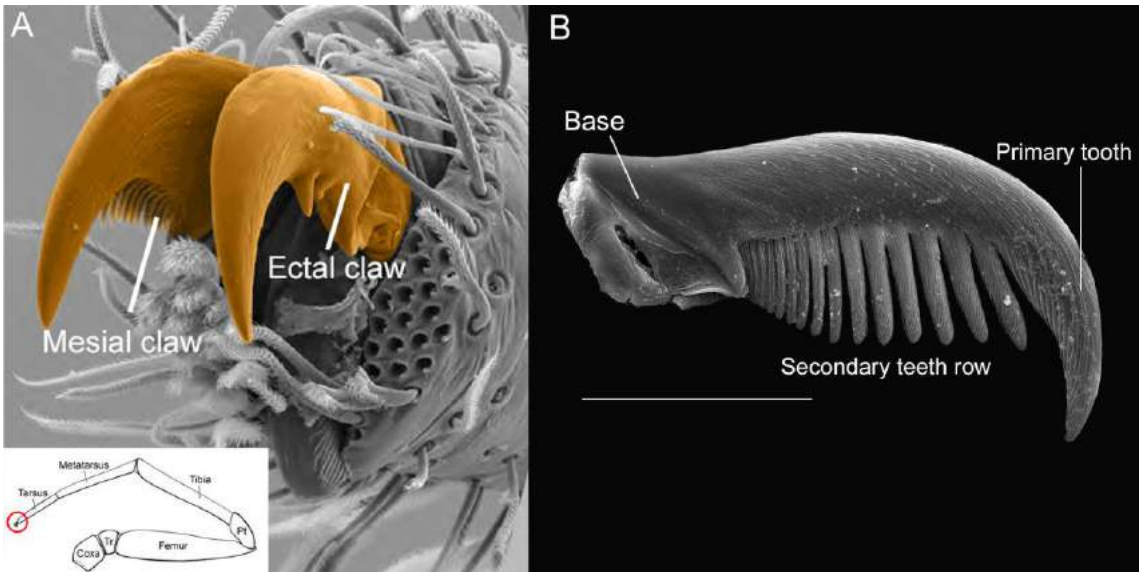
troncos e serapilheira, apresentando padrões de coloração crípticos que lhes permitem não serem detectadas (Heiling et al., 2005).

A maioria das espécies de Thomisidae forrageia e vive exclusivamente em partes aéreas de plantas arbustivas ou de grande porte. Isto exige que a aranha tenha capacidade de escalar e de se locomover, aderindo-se a estes substratos com precisão. Contudo, diversas espécies de Thomisidae apresentam redução ou ausência das cerdas adesivas em seu tarso fazendo com que sua capacidade de adesão em superfícies lisas seja bastante reduzida (Wolff e Gorb, 2012 e 2015). Isto sugere que as garras, nestes animais, possuem a função principal em auxiliar na escalada e em sua adesão ao substrato.

Hill (1977,1978, 2010a e 2010b), Wolff e Gorb (2012, 2015 e 2016) e Labarque et al. (2017) avaliam diversos aspectos morfológicos e funcionais das garras em diversas espécies de aranhas. Contudo, a morfologia e funcionalidade das garras em Thomisidae ainda é pouco explorada, abordada somente em poucos trabalhos filogenéticos englobando a família (e.g. Ramirez et al., 2014; Machado et al., 2017).

Portanto, o presente trabalho analisa morfológica e evolutivamente a estrutura das garras em Thomisidade, buscando responder as seguintes perguntas:(1) Em qual nível taxonômico a morfologia das garras varia? (2) Existe dimorfismo sexual como observado em outras características da família? (3) Diferentes pernas apresentam garras com diferentes formas? (4) As garras exibem sinal filogenético? (5) Existe correlação entre a forma da garra e substrato de forrageio das espécies?

O trabalho encontra-se redigido como manuscrito científico, e está formatado segundo as normas exigidas pelo periódico *Zoologischer Anzeiger.* O texto foi redigido na língua inglesa com o objetivo de aperfeiçoamento e de treino do autor, e será, posteriormente aos apontamentos e correções dos avaliadores, enviado para revisão gramatical.



Arrumar a parte (A) colocar as coisas em português.

Figura 1. (A) Canto inferior esquerdo: Esquema nomeando os podomeros das pernas das aranhas com a ponta do tarso circulada em vermelho. Microscopia eletrônica de varredura (MEV) do tarso com as garras identificadas e destacadas em laranja; (B) MEV da garra em vista prolateral com suas diferentes regiões identificadas, barra de escala em branco representando 100µm. (A) Esquema: editado de Foelix (2011). Imagem: editado de Ramirez (2014).

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CHARPTER1: Morphological and macroevolutionary analysis of tarsal claws in crab spiders (Thomisidae)

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Abstract

Here we studied the morphology of crab spiders (Thomisidae) tarsal claws, by a geometric and linear morphometric analysis, based on a data set of 50 species. The aim of the study was to compare the claw morphology among species in an evolutionary context. In additionally test the existence of sexual dimorphism, evaluate the claw morphology among different legs, verify the phylogenetic signal in claws morphology and test its correlation with the foraging substrate of the species. Our results suggest that claw morphology vary only at genus level, with rare exceptions in one or two claws of some genus, with phylogenetic close genera also maintaining several characteristics in common. As expected, due the high sexual dimorphism in most species of Thomisidae, sexual dimorphism was detected in claws of all analyzed species, generally related with the primary tooth curvature. In general, claw morphology of different legs corresponds to the leg patter described in literature for most Thomisidae species, with forelimbs (leg I e II) proportionally larger than hindlimbs (legs III e IV). Forelimbs' claws are larger and less curved than hind limbs claws. Different from the expected, only mesial claws of legs I and II presented phylogenetical signal greater than expected at random. An ambiguous result, once most phylogenetic close species and genera did not present significant differences in claw morphology. Substrate correlation was reported for ectal claw of leg

I and mesial claws of legs II, III and IV hindlimbs. We did not found a plausible explanation for this based in a biological pattern and, considering that species with different claw shape can forage in the same substrate, we conclude that forage substrate are not shaping the claw morphology by itself.

Keywords: Evolution; Geometric morphometrics; Comparative morphology; Phylogenetic Comparative Methods.

1. Introduction

Claws are important structures in arthropod life, usually located on tip of their locomotory appendages, being responsible for many of the interactions of these organisms with their habitat (Barrows, 1925; Labarque et al., 2017). These structures promote adhesion to a substrate or host, allow food capture and manipulation, assist in copulation behavior and offspring carrying, as well as handling materials for construction of shelters or traps (Schultz 1989; Dunlop, 2002; Wolff et al., 2015).

In spiders, each leg has a pair of upper claws that protrude from a thin flexible cuticular membrane, and a lower third claw, located below and between the upper claws, responsible for the manipulation of silk in the web construction (Barrows, 1925). Some spider families have reduced or lost this third claw, in different evolutionary events, being known as a functional group called Dyonicha (Ramírez, 2014).

Dionycha comprises 17 spider families, grouped based on the presence of only two tarsal claws (Petrunkevitch, 1928) and adhesive setae to climb on smooth surfaces (Ramírez, 2014). Within this group, there is Thomisidae, a family of ambush sit-and-wait spiders, known to forage in different parts of plants and in soil litter (Gawryszewski, 2014). In several Thomisidae species there is absence or reduction of adhesive setae, turning its adhesion ability on smooth surfaces quite poor (Wolff and Gorb, 2015). This

could suggest that claws play the major role in the adhesion of these spiders on to the substrate.

Although there are studies analyzing several morphological and functional aspects of claws in spiders (e.g. Hill, 1977a, 1977b,1978, 2006 and 2010; Wolff e Gorb, 20012, 2015 e 2016; Labarque et al., 2017), Thomisidae claws have been scarcely studied regarding their morphology and functionality. Currently, some studies include Thomisidae claw characteristics, such as number of secondary teeth, teeth projection position and symmetry between mesial and ectal claws, in (*e.g*. Machado et al., 2017; Ramírez, 2014); However, there are no studies evaluating issues such as sexual dimorphism, claw differentiation among legs, testing the phylogenetic signal of this character or even the relation of these structures with environmental factors, for example, with the foraging substrate.

Therefore, this paper is a comparative and macroevolutionary analysis of tarsal claws based on a morphological dataset of 50 crab spider species. The aim of this study was to compare, via morphometric analysis, the claw morphology in Thomisidae, exploring the following questions: (1) In what taxonomic level does the claws morphology vary?, (2) Is there sexual dimorphism in claws as observed in other traits in the group?, (3) Do different legs exhibit different claws' shapes? (4) Is there phylogenetic signal in claw morphology?, (5) Is the claw shape correlated with the foraging substrate of the species?

Despite being an exploratory study, we can raise some hypotheses: According to Alexander Ivanovitch Petrunkevitch observations in others spider families (Petrunkevitch, 1926), the number of teeth in claws and their shape is highly variable, changing by families and from genus to genus. Based on this, we expect that claw shape varies just in the intergeneric comparisons. Thomisids are highly dimorphic organisms,

with males and females presenting different lifestyles in many species (Vieira et al., 2017), so this could select for different tarsal configurations, including the claw shape. Thomisids forelimbs (legs I and II) exhibit specialization to catch prey, evidenced by retrolateral spines on tibiae and metatarsus, besides podomers significantly larger than in the hindlimbs (legs III and IV), whose function is mainly to fix the animal on to the substrate (Jackson, 1995). This difference in function and morphology, in fore and hind limbs, could also suggest a differentiation in the claw morphology. According to the hypotheses above, we expected to find a highly phylogenetic signal in the forelimbs' claws, while hindlimbs would be correlated with the foraging substrate of the species.,

2. Materials and Methods

2.1 Taxa selection and examined material

The taxa analyzed in this work includes Thomisidae species whose genera are comprised in the latest published phylogenetic analysis of Araneae (Wheeler et al., 2016). Excepting *Alcimocthes*, *Boliscus, Monaeses, Thomisops, Simorcus Stiphropus,* and *Talaus*, all others 27 genera are represented by at least one species. Some genera are represented with more than two species (e.g. *Acentroscelus; Epicadus; Misumenops; Strophius*), allowing intrageneric comparisons in the main branches of the phylogeny.

The study was conducted at the Laboratório de Aracnologia do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Brazil (MCTP) and it was based on 250 (145 females and 105 males) adult specimens preserved in 70% ethanol that were made available by the following institutions: American Museum of Natural History (AMNH, L. Prendini); Australian Museum (AMS, G. Milledge); California Academy of Science (CAS, L. Esposito); Forschungsinstitut und Naturmuseum Senckenberg (SMF, P. Jäeger); Instituto Butantan (IBSP, A. Brescovit);

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2.2 Claw preparation and image acquisition

Mesial and ectal claws of legs I-II-III-IV were dissected in dry, under an optical stereomicroscope, with help of a micro-scalpel and a pair tweezers. Each claw was fixed on a microscope slide coverslip (22mm x 22mm) using a thin layer of transparent nail polish as glue. Mesial and ectal claws were fixed in prolateral and retrolateral view, respectively. The microscope slides were divided in quadrants by using a permanent marker (0.05mm), each quadrant was identified with the number of the one of the legs (I, II, III or IV) and the claws were circled and identified with the letter M for mesial and E for ectal, just below the circle. Each microscope slides received an internal code, representing the specimen whose claws belonged, and they were fixed in pairs in larger microscope slides (75mm x 26mm) with a double-sided tape and packaged on a microscope slide box.

Each microscope slide pair was coated in gold with the Q150R ES-plus coater (Quorum) and subjected to a field emission scanning electron microscopy using the Inspect F50 (FEI) electron microscope from the Laboratório Central de Microscopia e Microanálises (LabCEMM) facility from PUCRS. Claws showing the base or primary

tooth broken or submerged in the glue were disregarded in the analysis.

2.3 Morphometric data

The images' set was used in landmarks (LM) and semilandmarks (sLM) digitization, and for obtaining the length and counting the number of secondary teeth of the claws. Length measurements were obtained using ImageJ2 (Rueden et al., 2017), LM and sLM were digitized using TpsDig2 software (Rohlf, 2015). For the digitization, the images were divided in 16 sets, by sex, leg (I, II, III or IV) and claw (mesial or ectal). Images were pseudoreplicated (add one copy) to consider margin of error in plotting of anatomical landmarks. Length metric example and landmarks (six LM and 20 sLM) disposing and definition are illustrated in Fig. 1.

After digitization, we built new TPS files to match *males vs. females* (matching same leg, claw and taxa) and *leg vs. leg* (matching same sex, claw and taxa). Each TPS file was superimposed with a Procrustes superimposition (GPA) (Adams et al., 2013). The sLM were slid, minimizing the bending energy (Perez et al., 2006). All geometric morphometric procedures were implemented using the *geomorph* package (Adams and Otárola-Castillo, 2013) in the R environment (R Core Team, 2016).

2.4 Substrate and Phylogeny

The foraging substrate data were taken from literature obtained via an advanced search performed on Google Scholar platform, using the following presets: **with all words:** [genus name] and **with at least one of the words:** "habitat" or "environment" or "ecology" or "substrate". The information comprised taxonomy works quoting the substrate where the specimen was found and collected, scientific notes with direct observation and photography registers of specimen preying or stalking, sample data of species inventories, unpublished PhD dissertations with direct collect information (hand

capture), and ecology studies. A list of consulted literature is provided in Appendix 2. To test the correlation between claw shape and substrate, only female morphology data were used, given that males have different life habits and may not share the same substrate as females, with poorly information available (Vieira et al., 2017). The substrate variable was constructed by assigning a part of the plant (Flower, Leaf or Branches) or Litter to each species, according to what has been most reported to the genera in the consulted literature. Intrageneric variation in substrate assignation was considered only when clear evidences were provided.

Morphology suffers influence of common shared ancestry and it is shaped by ecological and evolutionary processes (Losos and Miles, 1994). Therefore, we pruned the Wheeler et al. (2016) molecular tree, by taking just thomisids species relationship, building a *work tree*, to test the phylogenetic signal and the correlation between claw shape and the foraging substrate of the species.

The construction of the *work tree* followed the following steps: (1) species missing from Wheeler et al., (2016) phylogeny were grouped with species of the same genus or subfamily — e.g. *Bomis larvata* was grouped with *Boliscus cf. tuberculatus* following taxonomic remarks of Ono (1988); (2) unsampled species were cut off from the phylogeny; (3) branches containing polytomies, after the inclusion of taxa, were randomly solved using the *multsepai2di* function of *ape* package (Paradis E. and Schliep K. 2018) in the R environment (R Core Team, 2016). The branch lengths were maintained exactly as in the original phylogeny. The edited phylogeny and substrates assigned for each species are illustrated in Fig.2.

2.5 Statistical analyses

To answer the raised questions, the statistical analyses were divided into four blocks (see below). All MANOVA and pairwise tests were implemented using the *procD.lm* and *pairwise* functions respectively, both from *geomorph* package (Adams and Otárola-Castillo, 2013). The ANOVA and THSD tests were implemented using the *aov* and *TukeyHSD* function, both from *stats* package, native from R environment. The K tests and PGLS analyses were implemented using the *physignal* and *procD.pgls* functions respectively, both from the *geomorph* package (Adams and Otárola-Castillo, 2013). All routines were performed in the R environment (R Core Team, 2016).

(1) **Species vs. species:** This block included 16 multivariate analyses of variance (MANOVA), followed by pairwise tests, each one analyzing one of the 16 datasets described above in the "Morphometric data" section. The results of these analyses were used to verify the possibility of working with the specimens at genus level or the need to treat them as species separately for the following analyses.

(2) **Males vs. females:** Here we tested the occurrence of sexual dimorphism in homologous claws of individual legs using MANOVA test. Only taxa presetting a well number and both sexes sampled were analyzed. The results of these analyses were used to split or combine males and females' datasets in the following analyses.

(3) **Leg vs. leg:** Here we compared homologous claws among different legs. The shape was compared using MANOVA followed by pairwise tests for Procrustes shape variables, while length and number of secondary teeth were compared using analyses of variance (ANOVA) followed by Tukey Honest Significant Difference (THSD).

(4) **Phylogenetical signal and substrate-claw correlation:** Here we evaluated the phylogenetic signal for Procrustes shape variables, in each one of the claws of each one of the legs, considering just the female dataset used in *Species vs. species* block.

The phylogenetic signal was estimated using the generalized K statistic for multivariate data (K test) (Blomberg et al., 2003). The correlation between the claw shape and foraging substrate was tested with the same dataset using Phylogenetical Generalized Least Square (PGLS) analyses, based on Brownian motion models (Martins and Hansen 1997, Rohlf 2001).

3. Results

3.1 Species vs. species

To summarize the results of the 16 tables of MANOVA pairwise comparison (available in the Appendix 3), we calculated the percentage of comparisons presenting statistical difference (p-value<0.05) in each species match of all tables, building a unique table showing, in a color score rank, this percentage for each comparison (Fig.3). Most intrageneric comparisons did not show significant differences in claw shape, except for rare cases involving specific claws of one or two legs (see Appendix 3).

Furthermore, some phylogenetically close genera also did not show statistical differences in claw shape. In Aphantochilinae, only *Ceraarachne blanci* showed statistical differences in most comparisons with some species of the subfamily. In *Misumena, Xysticus* and *Epidius* clades all species showed no statistical difference in most pairwise comparisons between them. In *Tmarus* clade *Titidius galbanatus* showed statistical difference in most comparisons with species of *Acentroscelus*. In *Stephanopis* clade, statistical differences were observed when we compared *Epicadus caudatus, Stephanopis parahybana* and *Stephanopis pentacantha* with *Onocolus trifolius,* and *Epicadus heterogaster* with *Stephanopis pentacantha*.

Species of Aphantochilinae did not show significant statistical differences when compared with some species of *Tmarus* and *Xysticus* clade, while species of *Stephanopis*

clade did not show significant statistical differences in most comparisons with Borborpactinae and with *Coenypha edwardsi* and the *Sidymella* genus from *Epidius* clade.

3.2 Males vs. females

As in *Species vs. species* comparisons intrageneric statistical differences in claw shape were observed in just a few cases to specifically claws of one or two legs, following analyses were performed treating the taxa at the genus level. Sexual dimorphism was tested for the genera with the largest number of individuals sampled that presented both sexes analyzed: *Bucranium* and *Strophius* of Aphantochilinae; *Misumenops* of *Misumena clade; Tmarus and Titidius* of *Tmarus* clade; all genera composing *Stephanopis* clade; *Coenypha* and *Sidymella* of *Epidius* clade. Principal Component Analyses and MANOVA p-values are available in Appendix 4.

As expected, according to other high sexual dimorphic traits in Thomisidae (Benjamin, 2013; Machado et al., 2018), most genera, showed sexual dimorphism in claw shape of all claws in the four legs. In Aphantochilinae, *Bucranium* presented sexual dimorphism only in claws of hindlimbs (leg III and VI), while only claws of leg IV in *Strophius* did not show sexual dimorphism. In *Epidius* clade sexual dimorphism was not observed just in claws of leg IV of *Coenypha* and ectal claw of leg III of *Sidymella*.

3.3 Leg vs. leg

As in *Males vs females*' comparisons most genera showed sexual dimorphism in claws' shape, males and females were analyzed separately in this analysis. Here we included, beyond the genera cited in "*Males vs. females"* section, *Aphantochilus* (females) of Aphantochilinae, and *Acentroscelus* (females) of *Tmarus* clade, aiming to

increase the sample number with well sampled genera that did not have both sexes sampled. This resulted in 44 MANOVA pairwise comparisons for claw shape, 44 pairwise comparisons for claws' length and 44 pairwise comparisons for number of secondary teeth. Graphics and p-values are available in Appendixes 5 and 6.

3.3.1 Claws' shape

Our hypothesis was that significant differences would appear, only when hind and forelimbs' claws were compared with each other. This was corroborated in 59% of the MANOVA pairwise comparisons. Cases in which the expected pattern was partially redeemed, occurred in 15.9% of comparisons and were called "limit cases".

Expected pattern were corroborated to both claws (mesial and ectal) for males and females, in the following genera: *Epicadus, Onocolus, Stephanopis* and *Misumenops*. This pattern has still been found in both claws in females of *Acentroscelus*, *Bucranium* and *Coenypha*, and males of *Tmarus*. Ectal claws of males of *Strophius* and females of *Tmarus*, and mesial claws of *Sidymella*, also presented the predicted pattern. Limit cases include ectal claws of females of *Titidius*, *Strophius* and *Sidymella* and mesial claws of *Strophius* (males and females) and males of *Coenypha* and *Bucranium*. Cases that differ significantly from the expected pattern are observed in mesial and ectal claws of *Aphantochilus* and *Titidius* males, mesial claws of females of *Tmarus* and *Titidius*, and ectal claws of males of *Coenypha* and *Bucranium*, and females of *Sydimella.* Most of them, presenting single patterns of claw shape similarity, which will be covered in the discussion. Principal Component Analyses showing the p-value of ANOVA pairwise comparisons are available in Appendix 5.

3.3.2 Claw length and number of secondary teeth

In 76.19% of the comparisons performed, we found that, on average, forelimbs' claws are larger than hindlimbs' claws. Cases in which claws did not show a clear

significant differents in length, could be observed in *Bucranium* (both sexes), *Aphantochilus* (females), and males of *Titidius* and *Strophius*. Boxplots and bar plots illustrating claws' length and number of teeth with the p-values of THSD tests are available in Appendix 6.

A clear pattern in the number of secondary teeth was found in *Stephanopis* clade, in which the number of secondary teeth in mesial claws was higher in forelimbs than in hindlimbs, while in ectal claws, the number of secondary teeth was higher in hindlimbs than in forelimbs' claws. The same pattern on mesial claws was also found in *Misumenops*, *Tmarus* clade and *Epidius* clade. Genera of Aphantochilinae showed varying patterns in number of secondary teeth in both claws (see Appendix 6).

3.4 Phylogenetic signal and substrate-claw correlation.

The K tests showed phylogenetic signal greater than expected in the Brownian motion model ("strong phylogenetic signal") just for ectal claws of forelimbs (leg I, K = 1.1339; leg II, K=1.1314). All other claws presented a lower phylogenetic signal than expected in the Brownian motion model (K<1) (Fig 4 and 5) ("weak phylogenetic signal").

In PGLS analyses, mesial claws of legs II, III and IV presented correlation with the foraging substrate of the species (leg II, p-value: 0.039 / R^2: 0.168 ; leg III, p-value: 0.018 / R^2: 0.142 ; leg IV, p-value: 0.011 / R^2: 0.157), while in leg I only ectal claw presented strong correlation with the foraging substrate (p-value: 0.0008 / R^2: 0.160).

4. Discussion

4.1 Claw shape and length by leg

As hypothesized, claw shape and length follow the leg allometry pattern reported for most thomisids in taxonomy studies: forelimbs very similar in morphology presenting larger podomers than hindlimbs, that also do not present significant differences in morphology between them (e.g Xu et al., 2008 e.g. Benjamin, 2013; Machado et al., 2018;). In forelimbs of the Borborpactinae, *Epidius* clade, *Stephanopis* clade and *Misumena* clade genera, we could observe larger claws with larger and very distinct primary teeth with open internal curves (based in the comparison of the Procrustes superimposition). Forelimbs are raptorial (Jackson, 1995; Schmalhofer, 1999) presenting clear adaptations for food capture, as tibial and metatarsal spines, and femoral protuberances (Machado et al., 2018). Keeping this in mind, we think larger claws in open angles could assist promoting traction preventing prey from escaping, similar what is seen in raptorial legs of *Heterogriffus berlandi* (Thomisidae), whose mesial claw are larger than ectal claw (Platnick, 1976), representing a possible adaptation for prey capture (Wolff and Gorb, 2016).

In hindlimbs, those same groups present shorter claws with primary teeth in closer internal curves (based on the comparison of the Procrustes superimposition). The main function of Hindlimbs is to hold the spider in the substrate while forelimbs are involved to catching preys (Morse, 1981; Morse, 1985; Jackson, 1995; Heiling, 2004). Experiments with beetles on rough surfaces suggested that pretarsal claws can significantly increase friction, when asperity sizes are much bigger than the claw tip (Dai et al., 2002; Bullock and Federle, 2011). Based on it, we thought hindlimbs' claws could possess this differentiation in size and primary teeth curvatures to assist in spiders'

attachment to the substrate, working like a hook, preventing the spider to falling from its foraging station while preying.

Different from other thomisids, species of Aphantochilinae are described as myrmecomorphic organisms, with a different pattern in leg allometry: legs I, II and III similar in shape and size, while leg IV its larger and oriented backwards (Mello-Leitão, 1929; Teixeira et al., 2014). Therefore, we expected in this group leg I, II and III presenting claw shape similarity and leg IV significant different from them. Although *Strophius* (males and females) and *Bucranium* (females) corroborate or fit among the limit cases that corroborate the hypothesis of differentiation between fore and hindlimbs. Only ectal claws of males *Bucranium* present a similar pattern with the expected in Aphantochilinae: claws of leg I and II similar, claws of legs II and III similar and claw of leg IV significant different from all others. In *Aphantochilus* and mesial claws of *Bucranium*, claws' shape varied, presenting unexpected patterns, like claw of leg II and IV similar and claw of leg I and III significant different from each other and from the other two. We could not find a plausible biological explanation for these patterns, and they are probably reflecting sample errors or problem due to the reduced sample size. Other spurious cases like this were found in *Titidius* (all males and only mesial claws of females), *Tmarus* (mesial claws of females) and *Sidymella* (ectal claws of females).

4.2 Sexual dimorphism

Regarding the observed dimorphism in most of analyzed genera, we could see that males and females maintain the general shape of the claw, varying only in the claws' length and curvature of the primary tooth. Females usually have larger claws with primary teeth at more open internal curves than males (see Appendix 4). Thomisids are sit-and-wait predators, non-web building (Gawryszewski, 2014). However, silk is used in this

group to build nests, shelters, sensory vibration systems to localize preys and to promote support in cases of fall (Morse, 1985; Jackson, 1995; Anderson and Morse, 2001; Morse, 2007). Therefore, it is not uncommon to see crab spiders releasing silk threads wherever they go (Anderson and Morse, 2001; Morse, 2014). The main activity of the adult males, despite foraging, is the search for females, using several mechanical, visual, and chemical clues to find them (Anderson and Morse, 2001). According to Anderson and Morse (2001), male crab spiders walk on silk threads left by females to follow them. We think this sharp curve in males' primary teeth claws could represent an adaptation to assist the locomotion following the silk threads left by females or their own (Anderson and Morse, 2001). Perhaps, it works as the median hook-like claw of in orb-web spiders (Wilson, 1962).

4.3 Number of secondary teeth

Despite the pattern found in number of secondary teeth in *Stephanopis* clad*e*, this character proved to be quite variable between genera. However, we could observe basal genera exhibit more disparity in the number of secondary teeth between mesial and ectal claws of forelimbs than in derived genera (Fig 6). Most groups analyzed in this work presented mesial claws of forelimbs with more secondary teeth than in ectal claws, with vary rare exceptions. For example, In *Epicadus*, we could observe many (14–21) tiny secondary teeth grouped in mesial claws, while in ectal claws we could observe few (1-3) robust secondary teeth, while in *Tmarus*, mesial claws present 14 –18 secondary teeth and ectal claws present 9–12 secondary teeth.

In the phylogenetic hypothesis proposed by Ramirez (2014), it is coded a character named "Superior tarsal claws I teeth symmetry", whose states were: (0) for: both claws similarly toothed; and (1) for: retroclaw (here called ectal claw) with many fewer teeth

than proclaw (here called mesial claw). State 1 it was scored for species within Thomisidae (most of them), Salticidae and Philodromidae (sister group of Thomisidae in this phylogeny) and of the genus *Zoropsis* (Zoropsidae). A functional explanation for this dissimilarity in number of secondary teeth was provided by Hill (2010), who analyzed the feet of jump-spiders in a very robust study based on morphological analyses and field direct observations, concluding that claws' primary teeth provide additional grip in climbing, but secondary teeth have the main (or exclusive) function of supporting the handling and securing silk lines. Thus, the many tiny secondary teeth with reduced inter spaces, seen in mesial claws (fig. 11D, pag. 12 of Hill, 2006), may be an adaptation to hold and guide the silk lines.

In Thomisidae, that dissimilarity is clearer in forelimbs' claws, but the reduced inter spaces between secondary teeth of mesial claws are found in all legs. As cited in "*4.2 Sexual dimorphism*" section, males thomisids use silk lines to find and follow females (Anderson and Morse, 2001), while females build nests, shelter and guide threads, (Morse, 1985; Jackson, 1995; Anderson and Morse, 2001; Morse, 2007), activities that require a certain degree of handling of the silk (Anderson and Morse, 2001). This corroborates with the function explanation provided by Hill (2006).

However, in the most recent molecular phylogeny of Araneae (Wheeler et al., 2016) Thomisidae was recovered within a clade called "Oval Calamistrum clade", as sister group of Psechridae, whose claws are not asymmetric in number of secondary teeth (Ramirez, 2014). While Salticidae was recovered as a derived clade, sister group of Philodromidae and Eutichuridae. This implies in an evolutionary convergence to claw teeth asymmetry in this groups, arising possible from the selective pressure for the habit of silk handling.

4.4 Phylogenetic signal and substrate correlation

The presence of phylogenetic signal only in ectal claws of forelimbs, seemed somewhat ambiguous with pairwise MANOVA results, once that closer genera did not show significant differences in most claw shape comparisons, with rare exceptions. However, absence of phylogenetic signal in mesial claws of forelimbs could indicate some select pressure shaping this character, for example, mesial claws may be correlated with the prey function (Platnick, 1976; Gillespie, 1991; Wolff and Gorb, 2016). Ectal claw of leg I also showed correlation with the substrate, which give us a clue that the foraging substrate may be driving the evolution history and, therefore claw's shape. Although it is unexpected that claws of leg II showed different responses of leg I regarding the correlation with the substrate, once that they did not show significant differences in *Leg vs. leg* comparisons. We think these results may have been influenced by the lack of sampling in the claws of leg II, due losses during preparation or the absence of the leg or claws in the specimens available.

Despite the shape of mesial claws of hindlimbs presented correlation with the substrate, ectal claws did not. It could suggest that mesial and ectal claws are subject to different selective pressures. However, the main difference between the two claws is in number and the sturdiness of the secondary teeth, something that was not directly evaluated in the substrate correlation tests. In addition, primary tooth curvature and insertion of claw base in tarsus its very similar in both claws, so the level of contact with the substrate it is probably the same for both claws (Hill, 2010). Considering that, we do not see a biological sense in just one of the claws being correlated with the substrate. As reported in previous works (Hill, 2010), claws primary tooth possess the main function of substrate grip, while secondary teeth function is to manipulate the web. However, species presenting different claws primary tooth shape can occupy same foraging

substrate, for example *Epicadus caudatus* (see fig.9) and *Tmarus litoralis*, (see fig. 11) or *Borboropactus divergens* and *Xysticus* sp., what indicate primary tooth shape are not correlated with the substrate usage by itself.

Despite the absence of adhesive setae, some species of Thomisidae present false claw tufts, a set of frictional setae, not too dense, that help in dry adhesion (Wolff and Gorb 2012 and 2015). Lapinski and Tschapka (2013) showed that large tropical hunting spiders of the grade-shaped tapetum clade differ in morphology of subungual seta according to the stratum they inhabit, with the arboreal species having good adhesive capacity and the ground dwellers having poor adhesion. Therefore, further studies should maybe evaluate the substrate correlation combining other tarsal characteristics, such as number of secondary teeth and quantity and type of subungual bristles, in addition to the claws' shape.

5. Morphological Description

The shape of the claws is described based on the *bauplan* found in each clade. Mesial and ectal claws of legs I and III of one species per clade were used to illustrate differences among fore and hindlimbs' claws. In addition to our personal observations raised, the following morphological characters are also evaluated in this description: (1) Claw teeth disposition: Restricted to the basal portion of the claw; Exceeding half of the claw length (Character 55 of Machado et al., 2017); (2) Superior tarsal claws teeth symmetry: Both claws similarly toothed; Retroclaw (ectal claw) with many fewer teeth than proclaw (mesial claw) (Character 139 of Ramírez, 2014); (3) Superior tarsal claws teeth insertion line: External margin; Median margin; Internal margin (Fig. 7) (Character 141 of Ramírez, 2014). Claws are described from the basal to the derived branches.

Borboropactinae: Both claws presenting primary tooth considerably larger than secondary teeth and more curved in the hindlimbs' claws. Secondary teeth row restricted to the basal portion of the claw, in mesial claws grouped in a defined patch near a one larger distinct secondary tooth (Ramírez, 2014). Ectal claws presenting many fewer secondary teeth than mesial claw. Secondary teeth row insertion line it is in external margin (Fig. 8).

Epidius **clade:** Primary tooth larger than secondary teeth and more curved in hindlimbs' claws. Secondary teeth row exceeding half of the claw length. Mesial claws presenting many same sized very small secondary teeth, with the last being distinctively larger than the others, while ectal claws present few robust teeth in a clear ascending row. Secondary teeth row insertion it is in external margin (Fig. 9).

Stephanopis **clade:** Both claws presenting primary tooth considerably larger than secondary teeth and more curved in the hindlimbs' claws. Secondary teeth row is restricted to the basal portion of the claw. Forelimbs ectal claws presenting many fewer secondary teeth than mesial claws, while in hindlimbs' claws are similarly toothed. Forelimbs mesial claws present many same sized very small secondary teeth, while ectal claws present few (1-3) teeth in a slightly ascending row. Hindlimbs' claws have secondary teeth in a clear ascending row. Secondary teeth row insertion line it is in external margin (Fig. 10).

Xysticus **clade:** Primary tooth presenting slightly less than twice the size of the largest secondary tooth. Secondary tooth row exceeding half of the claw length. Claws are similarly toothed, although mesial claws every present one or two more teeth, besides to smaller and less widely spaced teeth at the beginning of the row. Secondary teeth are disposed in a slightly ascending row, with the largest tooth being generally the penultimate. Secondary teeth row insertion is in medial margin (Fig. 11).

***Tmarus* clade:** *Tmarus* and *Titidius* present elongated claws with primary tooth larger than secondary teeth, while *Acentroscelus* present short and curved claws. Secondary teeth row exceeding half of the claw length, sometimes overlapping the primary tooth (mainly in *Titidius* and *Acentroscelus*). Mesial claws have more secondary teeth, in very small sizes at the beginning of the row, although in hindlimbs, the disparity in secondary teeth number is smaller. In this clade, secondary teeth are disposed in an alternate row, most evident in *Titidius,* in which the teeth remain ascending to the central region or close to the most basal part of the claw and begin to decrease in the direction of the primary tooth. Secondary teeth row insertion line is in internal margin in *Titidius* and *Tmarus*, while in *Acentroscelus* is in external margin (Fig. 12).

***Misumena* clade:** Both claws present primary tooth considerably larger than secondary teeth and more curved in the hindlimbs' claws. Secondary teeth exceeding half of the claw length. Mesial claws of forelimbs more toothed, presenting very small secondary teeth in the basal portion of the row that increase abruptly from middle to the distal portion of the row. Hindlimbs' claws similarly toothed, with mesial presenting one or two more teeth. Secondary teeth arranged in an ascending row inserted in external margin (Fig. 13).

Aphantochilinae: Elongated claws presenting primary tooth considerably larger than secondary teeth. Secondary teeth exceeding half of the claw length, slightly overlapping the primary tooth. Ectal claws presenting many fewer secondary teeth than mesial claws. Teeth are same sized in mesial claws with slightly larger teeth next to the primary tooth, while in ectal claws secondary teeth are disposed in a clear ascending row. Secondary teeth insertion line is in external margin in mesial claws and is in the internal margin in ectal claws (Fig. 14).

6. Conclusions

Resuming the key question that guided this study: (1) In what taxonomic level does the claws morphology vary? Our results demonstrate that claws' shape vary only at genus level in Thomisidae; however, phylogenetic closer genera maintaining several characteristics in common; (2) Is there sexual dimorphism in claws as observed in other traits in the group? Sexual dimorphism is presented in most genera analyzed, with males usually presenting closer curved claws than females; (3) Do different legs exhibit different claws' shapes? The claws' shape follows the allometry pattern found in most Thomisidae, with legs I and II largest and similar and legs III and IV shorter and similar. Hindlimbs' claws in addition to being smaller, were more curved, which indicates a possible adaptation to substrate grip (Wolff J. O., and Gorb, 2016); (4) Is there phylogenetic signal in claw morphology? Here a strong phylogenetic signal was found only in ectal claws of forelimbs, an ambiguous result when compared with the MANOVA pairwise comparisons among species, that demonstrate phylogenetic closer species and genera showing no significant differences in most claw shape comparisons. Although we used the most recent Thomisidae phylogenetic hypothesis to perform the Phylogenetic Comparative Methods, there is a great lack of information on species level relationships within this family, in addition to genera whose phylogenetic position has never been tested, which may be interfering in the analyses. (5) Is the claw shape correlated with the foraging substrate of the species? Substrate correlation was reported for ectal claw of leg I and mesial claws of legs II, III and IV. We did not found a plausible explanation for this based in a biological pattern, considering that species with different claws' shape can forage in the same substrate, we can say that claw shape primary tooth is not correlated with the forage substrate by itself, being perhaps necessary an evaluation additional tarsal

characteristics, such as the secondary teeth and the presence of subungual seta, besides its morphology and density.

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FIGURES

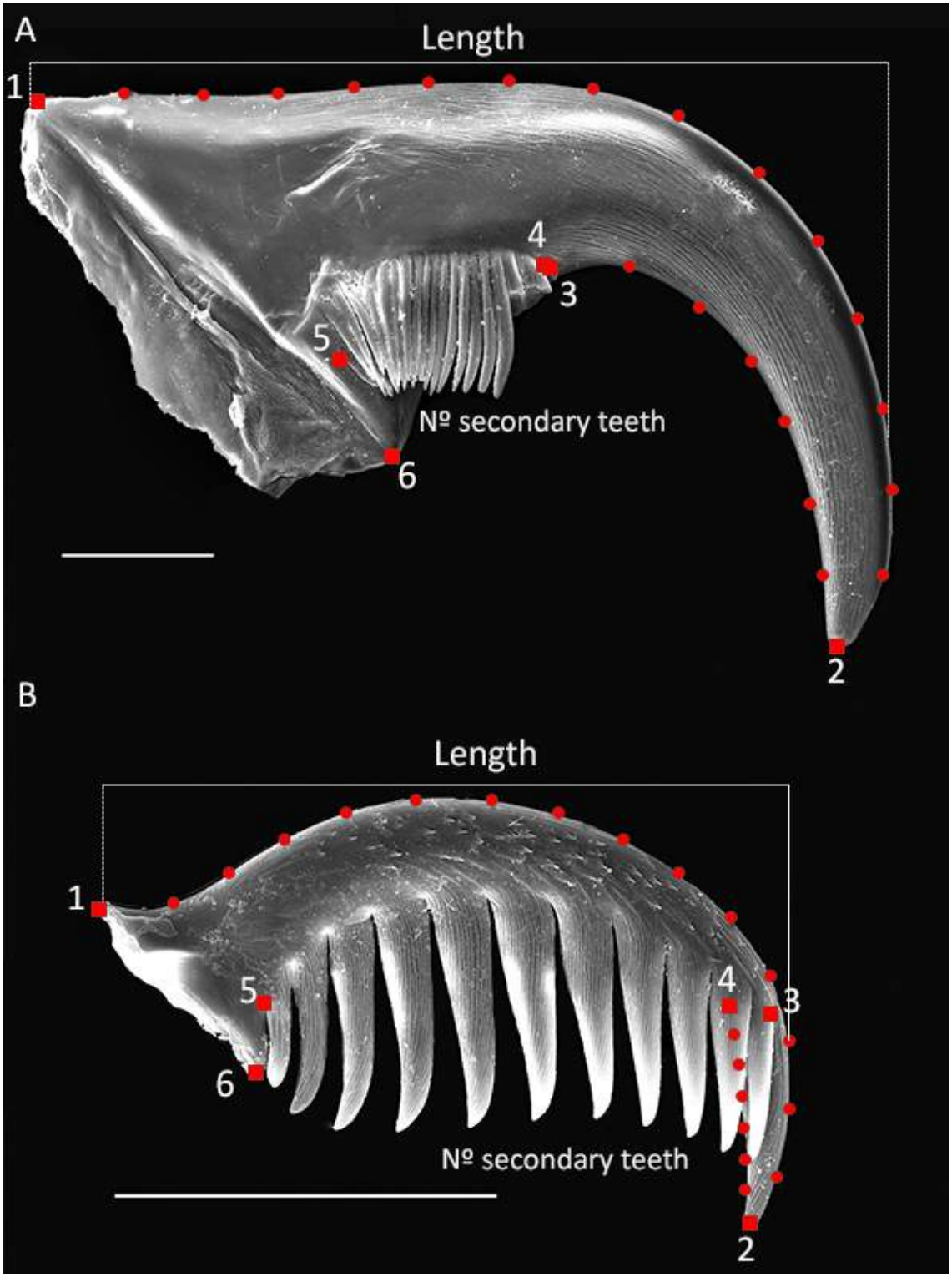

Figure 1. Position of the landmarks (squares) and semilandmarks (circles) digitized on the prolateral view of claws, with an example of length measurement. (A) Mesial claw of an *Epicadus heterogaster* female, (Leg I). (B) Mesial claw an *Acentroscelus albipes* female, (Leg I). White bars below claws represent 100µm scale. LM1: Superior tip of claw base; LM2: Tip primary tooth; LM3: End of primary tooth; LM4: Beginning of secondary teeth row; LM5: End of secondary teeth row; LM6: Inferior tip of claw base; sLM between LM1 and 2: External curve of primary tooth; sLM between LM2 and 4: Internal curve of primary tooth.

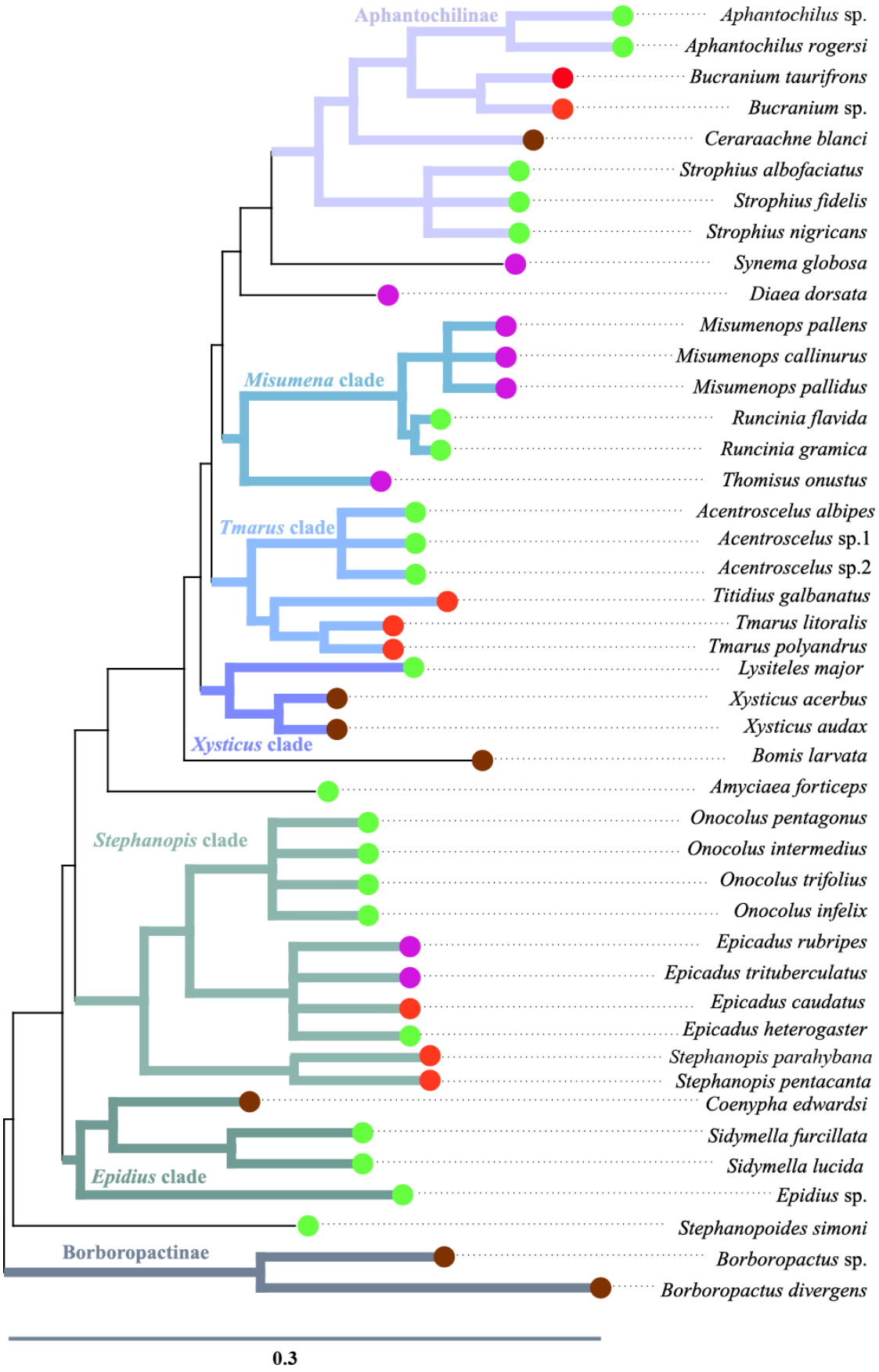

Figure 2. Phylogeny used in Comparative Phylogenetic Methods analysis, showing substrate assigned for each species. Terminal spheres: Green (leaf foraging group); Red (Trunk foraging group); Brow (Soil foraging group); Purple (Flower foraging group) Tree edited from Wheeler et al. (2016).

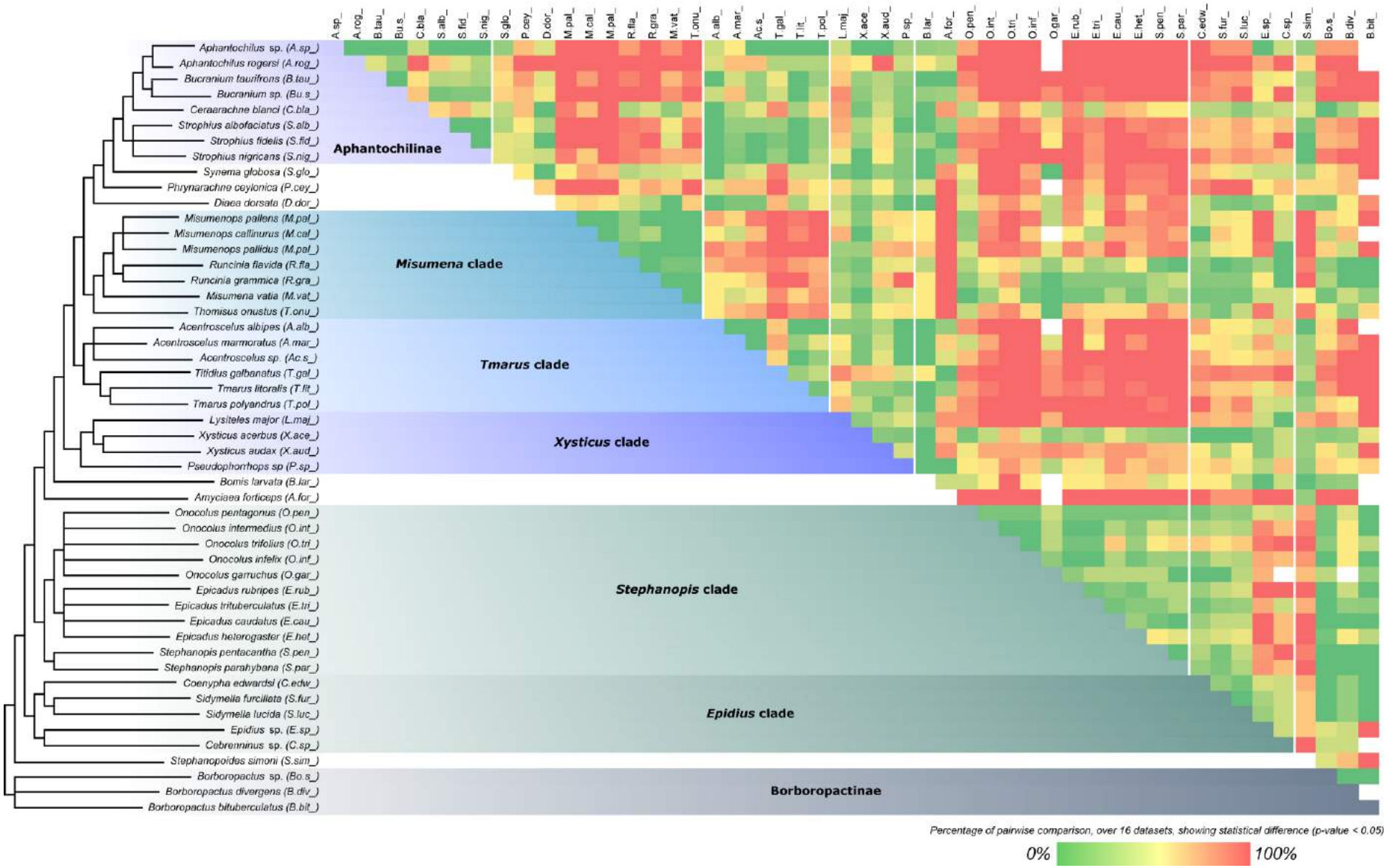

Figure 3. Table summarizing the16 tables showing the p-value of MANOVA pairwise comparisons of *Species vs. species*. The table shows the percentage of pairwise comparisons showing statistical differences. Green tones in the table represent species that showed no significant differences in most claw shape comparisons, while red tones represent species that showed significant differences in most claw shape comparisons. The phylogenetic relationship of species is shown in left.

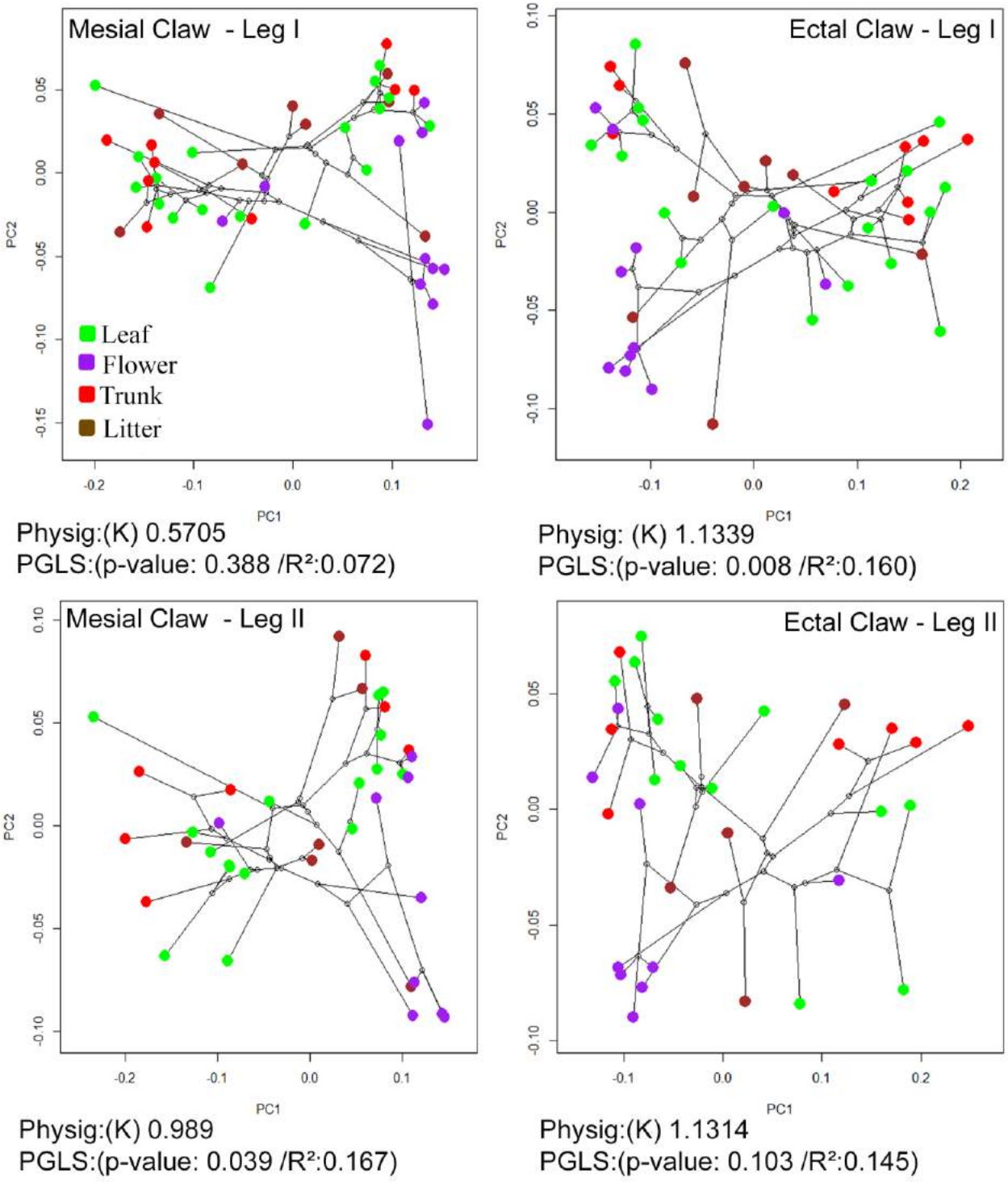

Figure 4. Principal component analysis of forelimbs' claws with phylogeny and substrate mapped. Below graphics are shown the K value of phylogenetic signal and the p-value and R^2 of PGLS analysis. The R^2 shows the percentage of the shape variation explained by the substrate.

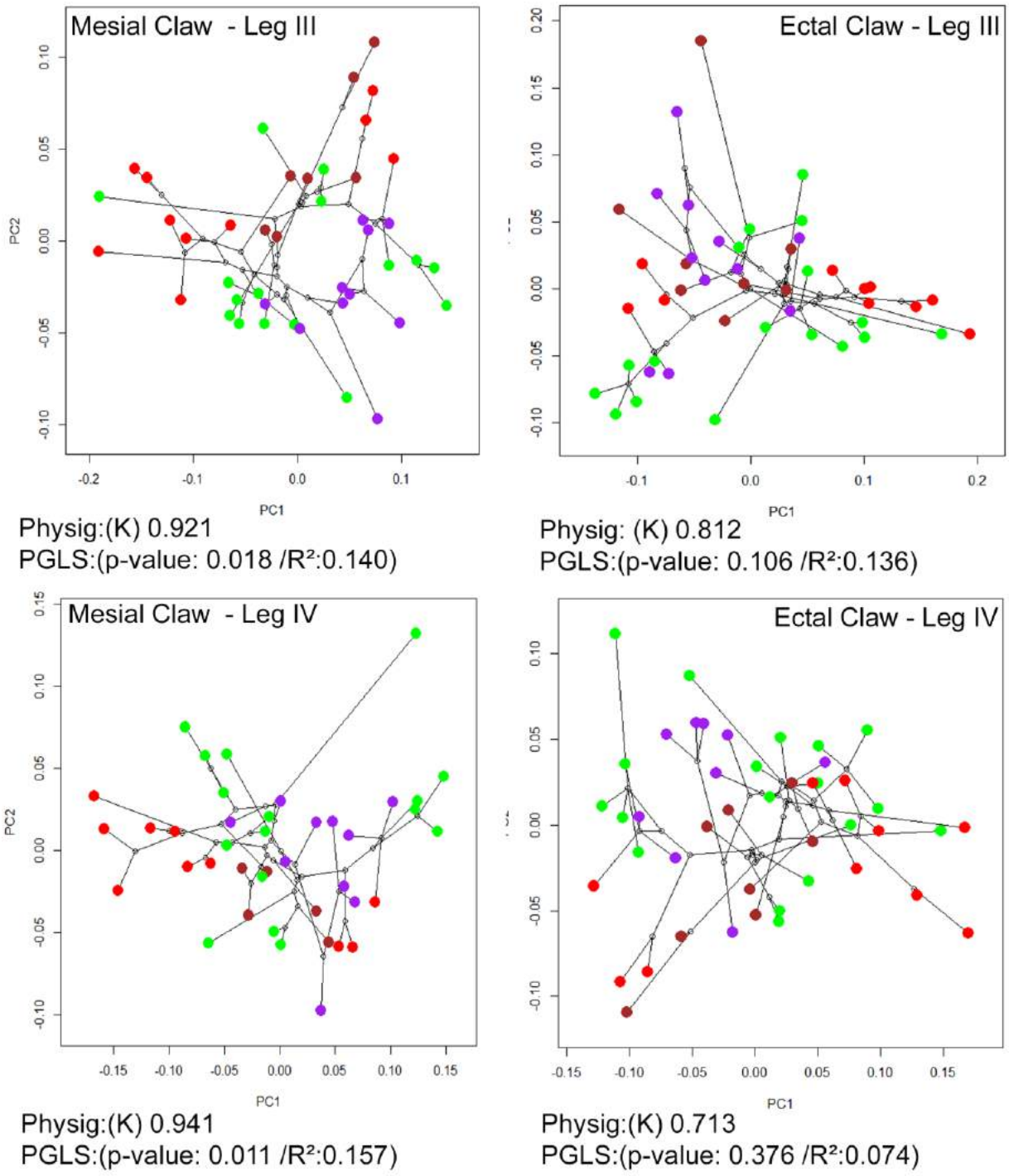

Figure 5. Principal component analysis of hindlimbs' claws with phylogeny and substrate mapped. Below graphics are show the K value of phylogenetic signal and the p-value and R^2 of PGLS analysis. The R^2 shows the percentage of the shape variation explained by the substrate.

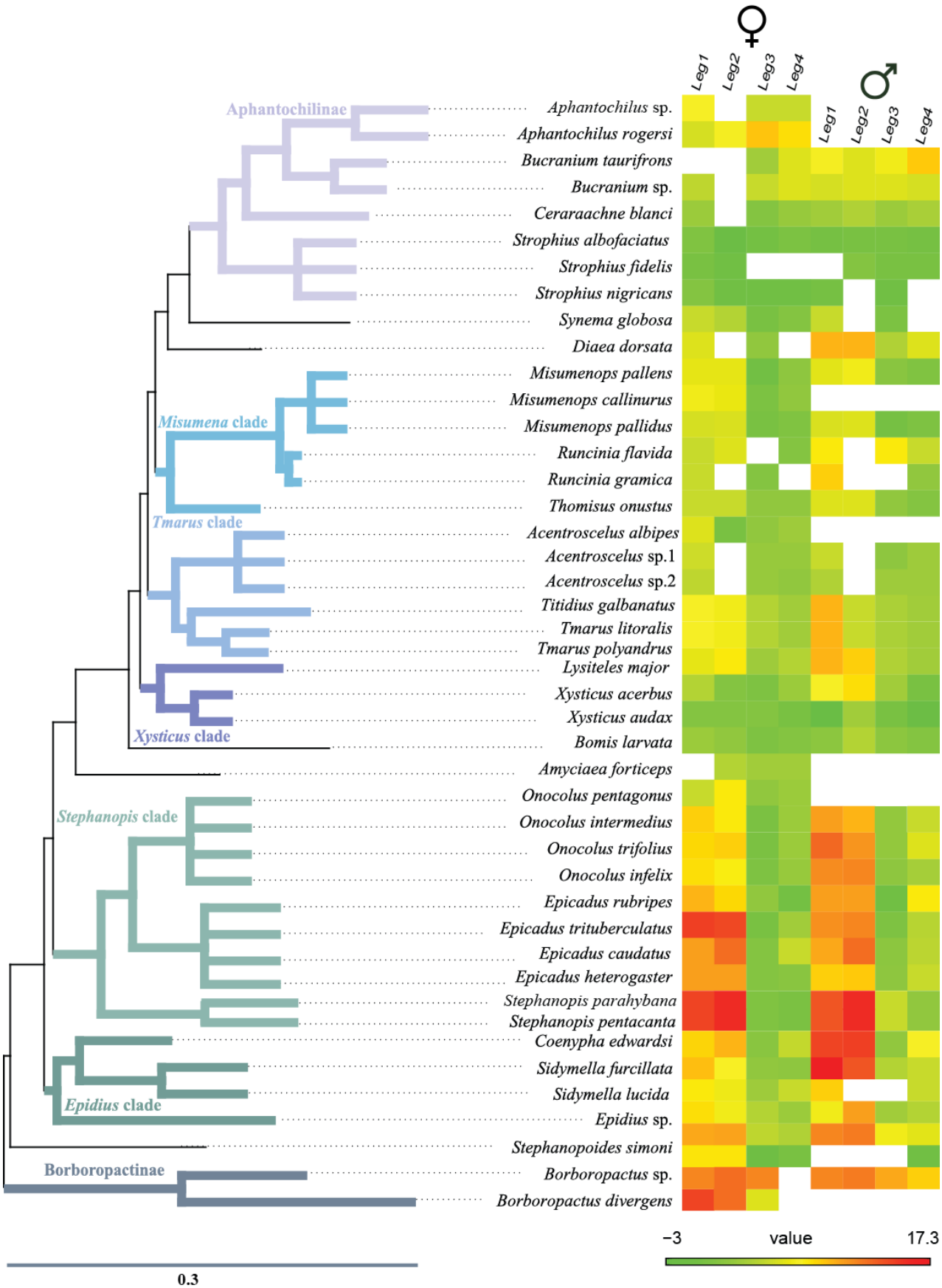

Figure 6. Disparity in number of teeth in mesial and ectal claws in each leg of males and females, mapped on the phylogeny. Green, yellow, orange, and red tones represent an increasing scale of disparity.

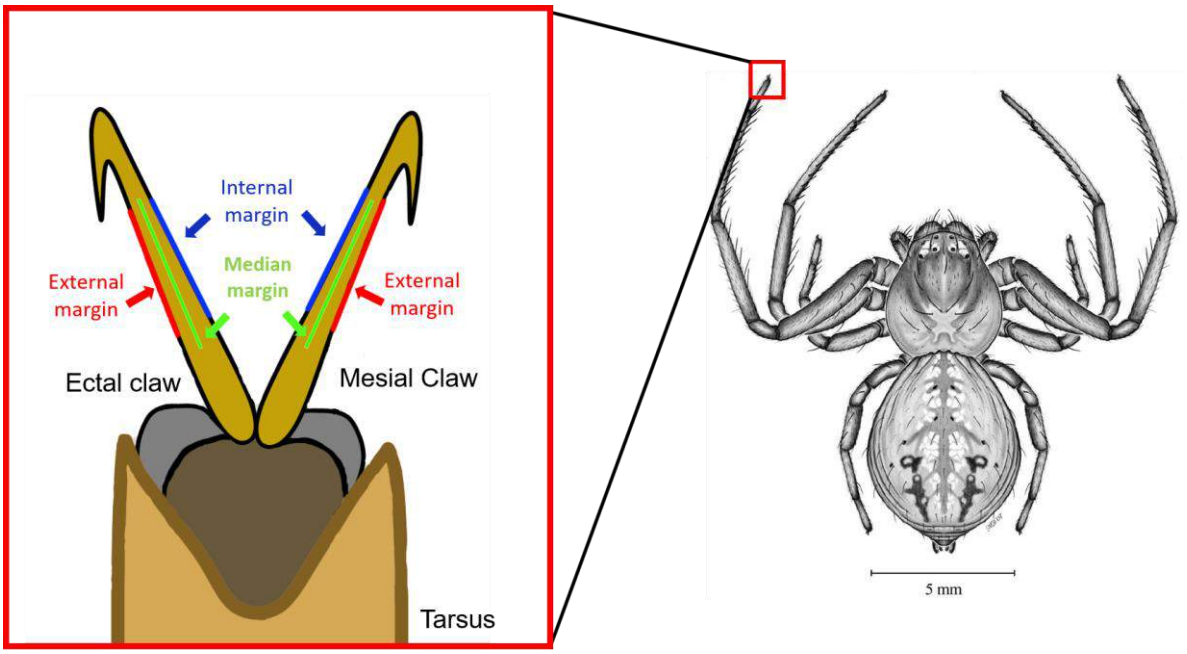

Figure 7. Scheme enlarging the tarsus of a crab spider illustrating the positioning of the claws and the insertion lines of the rows of second teeth. Crab spider illustration edited from (Cokendolpher, J. C. 2008). Arachnids associated with wet playas in the Southern High Plains, Llano Estacado, USA (No. 54). Museum of Texas Tech University.

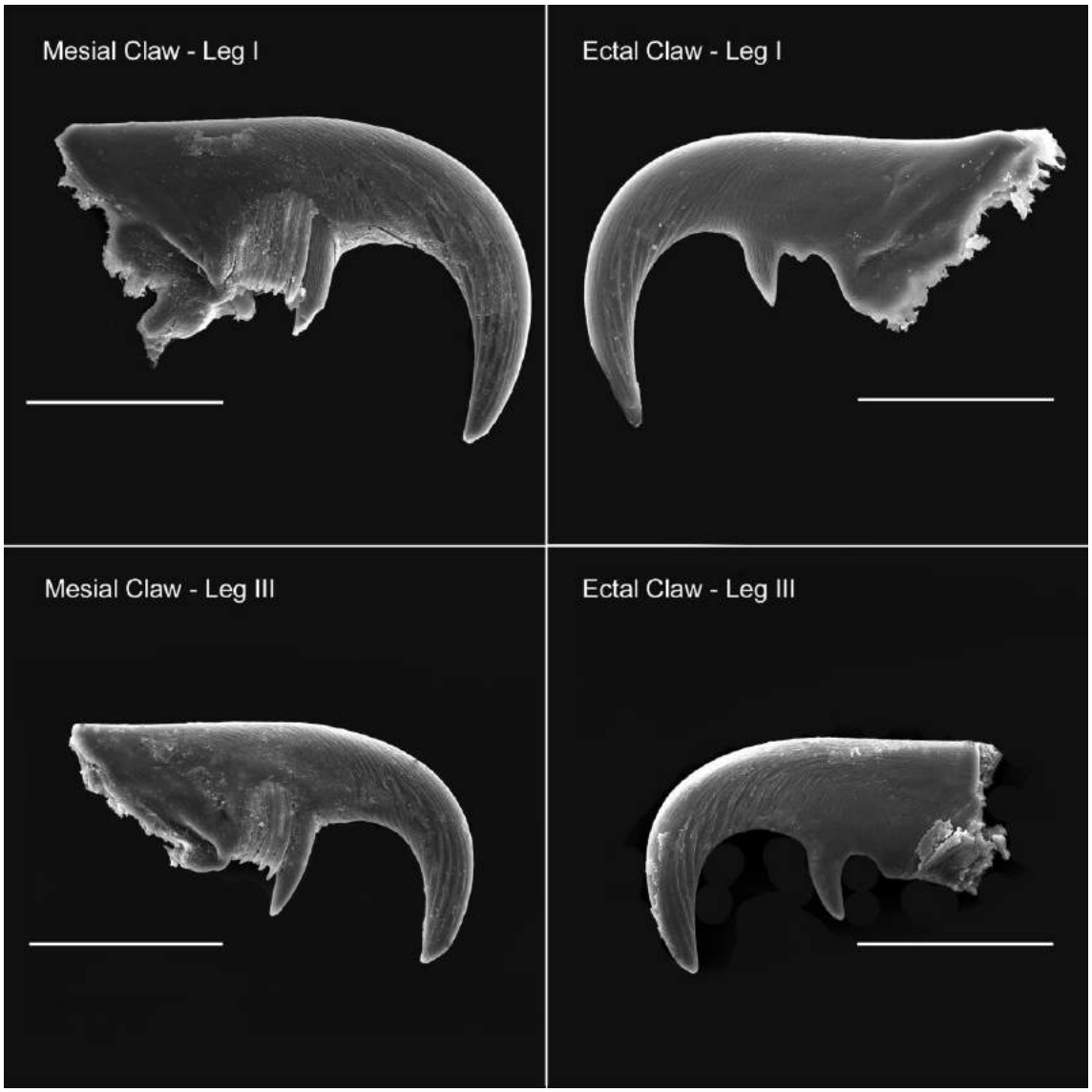

Figure 8. Mesial and ectal claws of leg I and III of *Borboropactus divergens* female, representing the general *bauplan* of claws found in Borboropactinae. White bars below represent 100 µm scale.

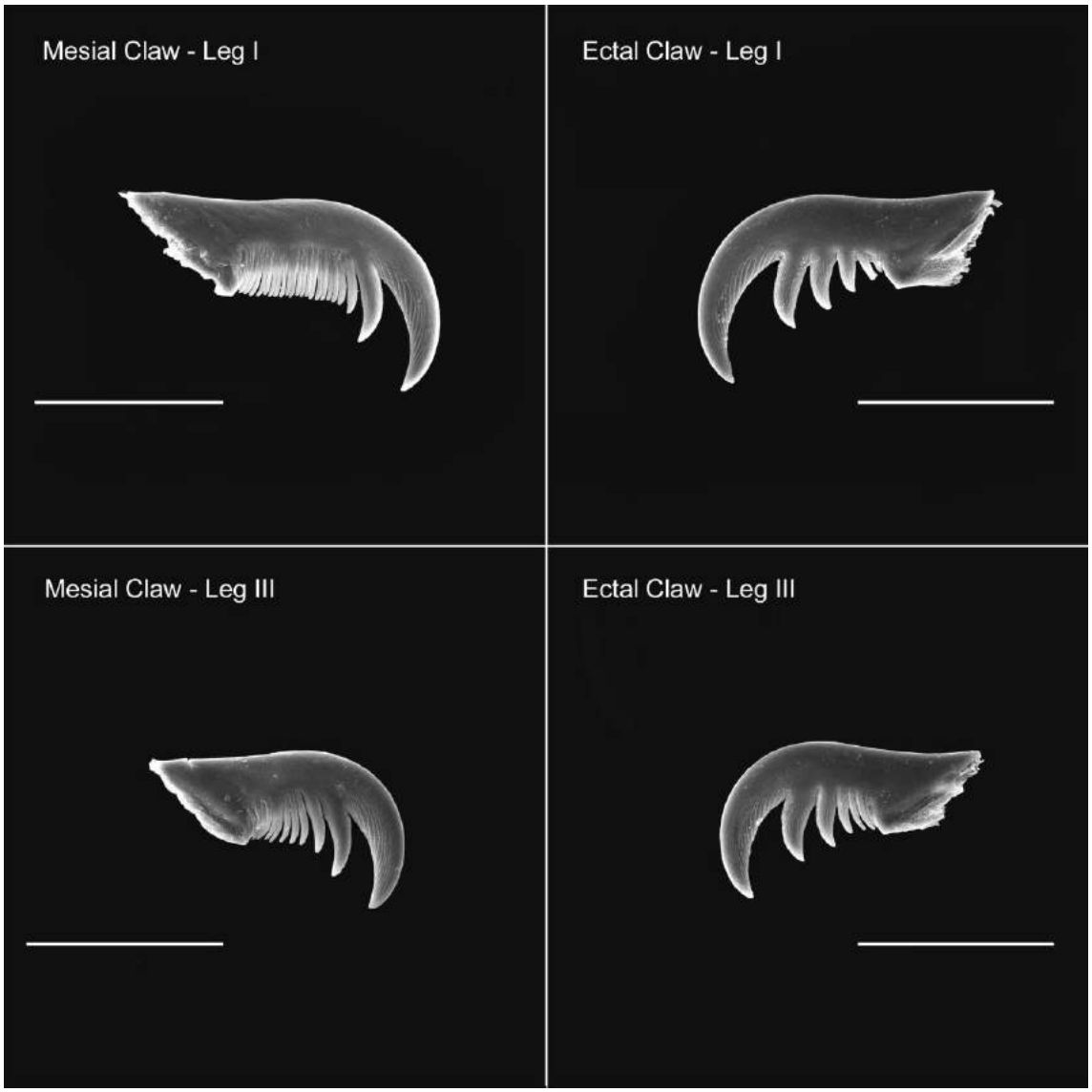

Figure 9. Mesial and ectal claws of leg I and III of *Coenypha edwardsi* female, representing the general *bauplan* of claws found in *Epidius* clade. White bars below represent 100 µm scale.

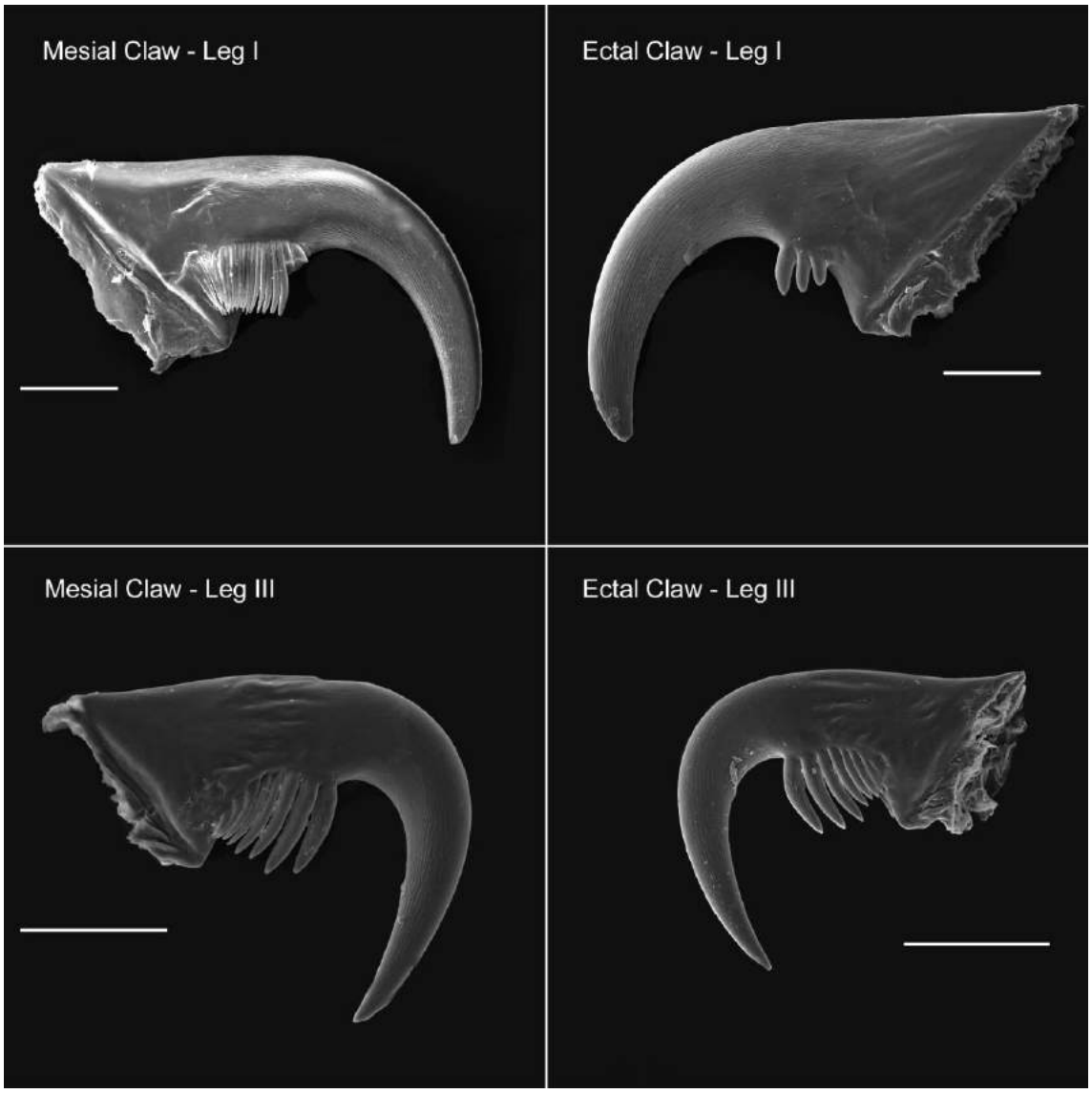

Figure 10. Mesial and ectal claws of leg I and III of *Epicadus heterogaster*, female representing the general *bauplan* of claws found in *Stephanopis* clade. White bars below represent 100 µm scale.

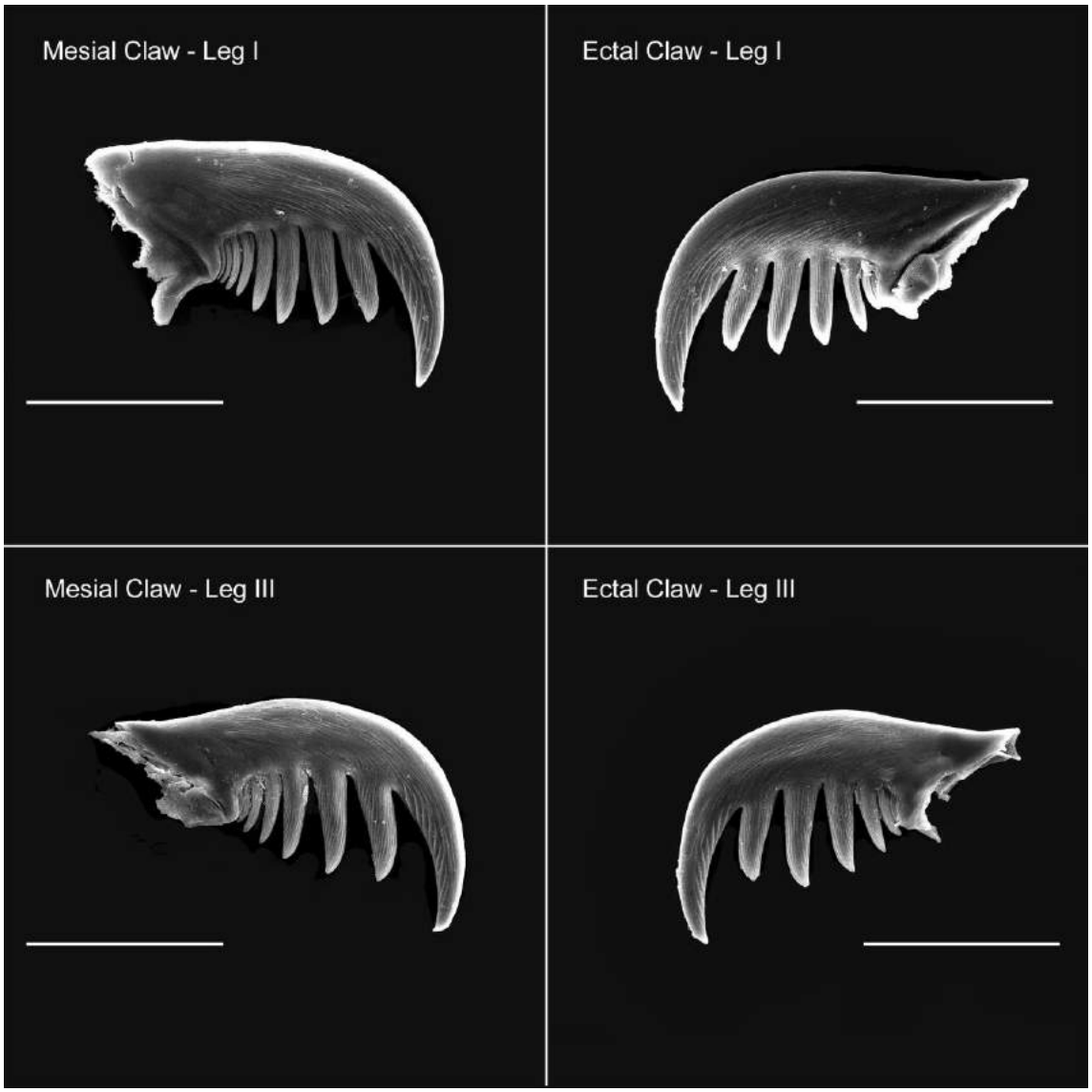

Figure 11. Mesial and ectal claws of leg I and III of *Xysticus audax* female, representing the general *bauplan* of claws found in *Stephanopis* clade. White bars below represent 100 µm scale.

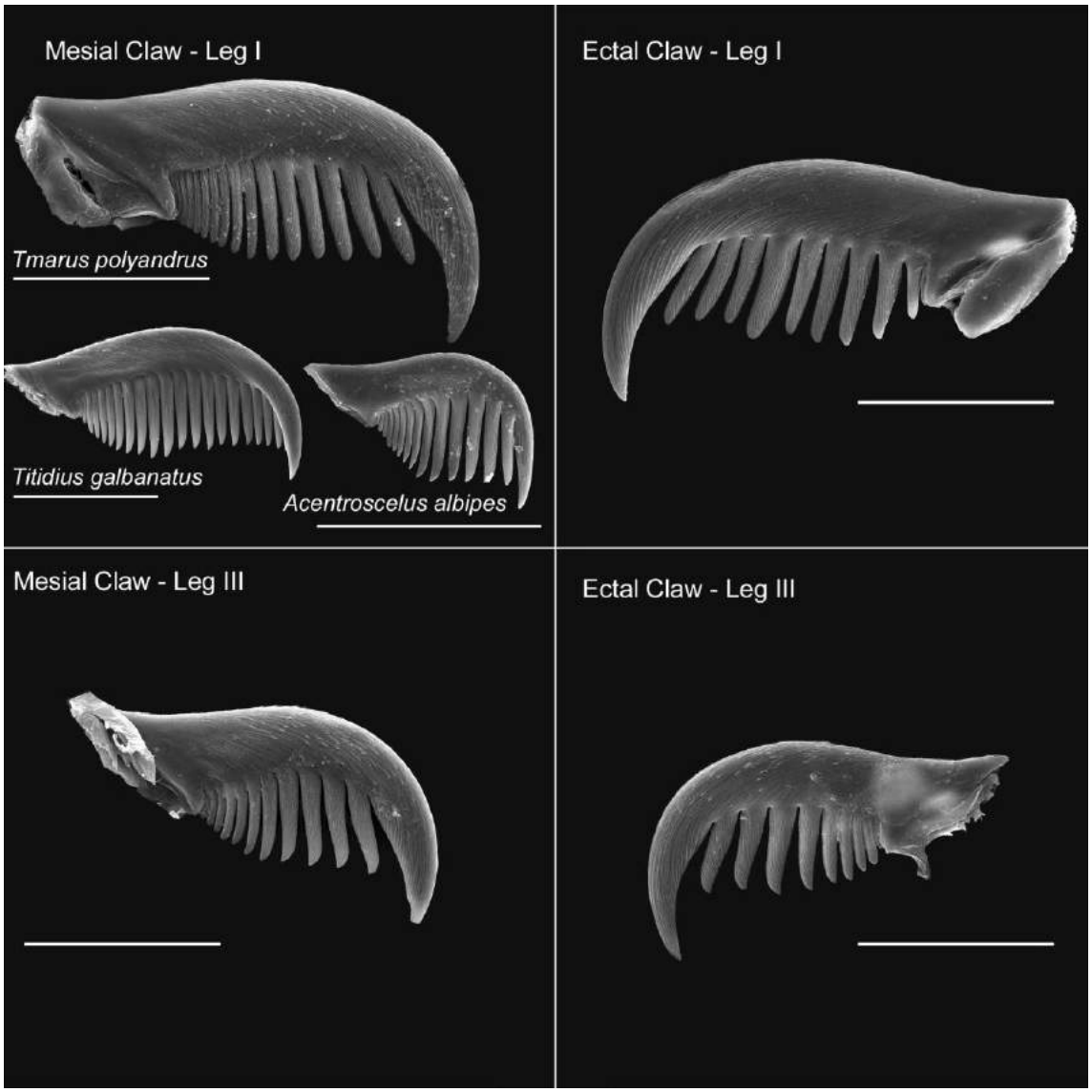

Figure 12. Mesial and ectal claws of leg I and III of *Tmarus polyandrus* female, representing the general *bauplan* of claws found in *Stephanopis* clade. White bars below represent 100 µm scale.

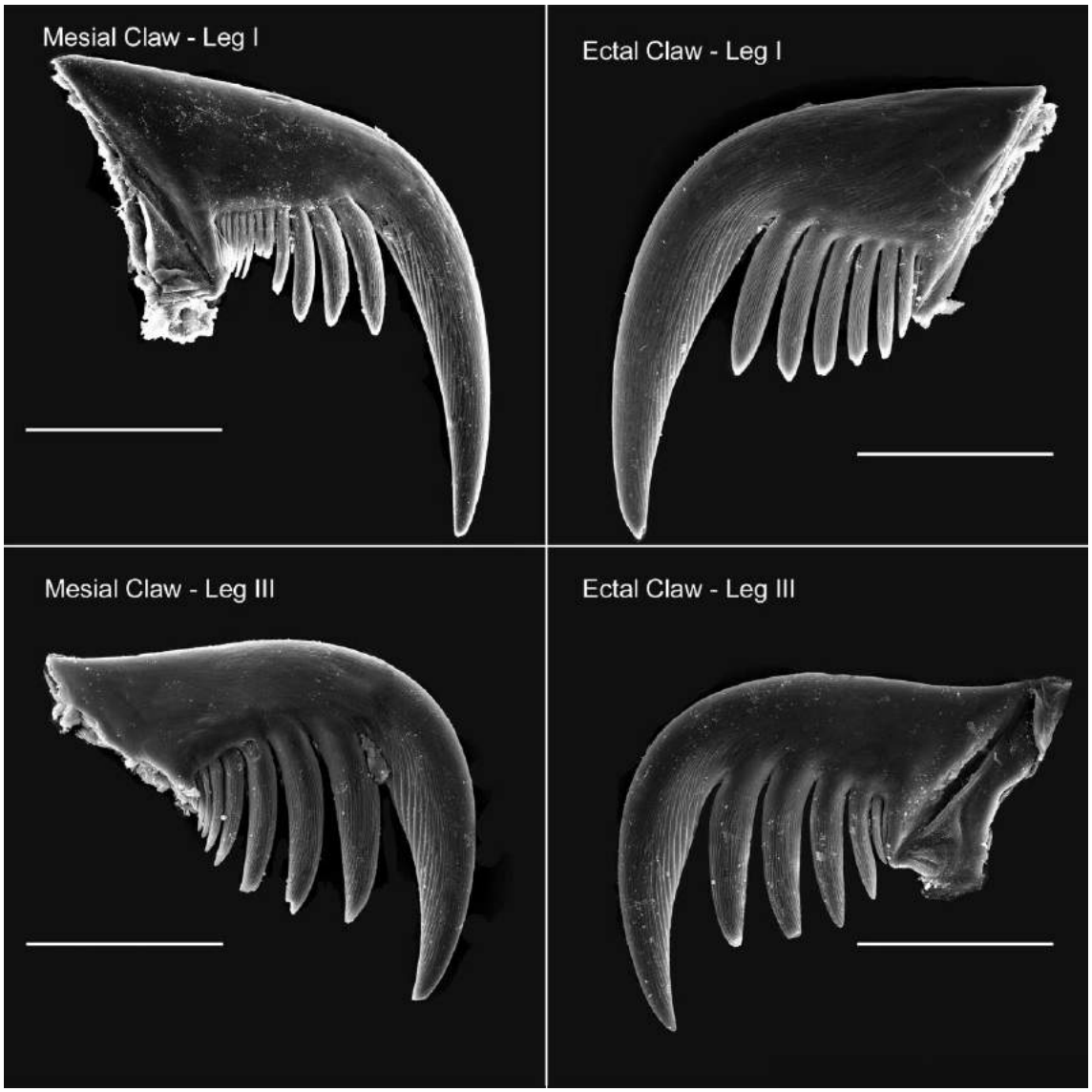

Figure 13. Mesial and ectal claws of leg I and III of *Misumenops pallens* female, representing the general *bauplan* of claws found in *Misumena* clade. White bars below represent 100 µm scale.

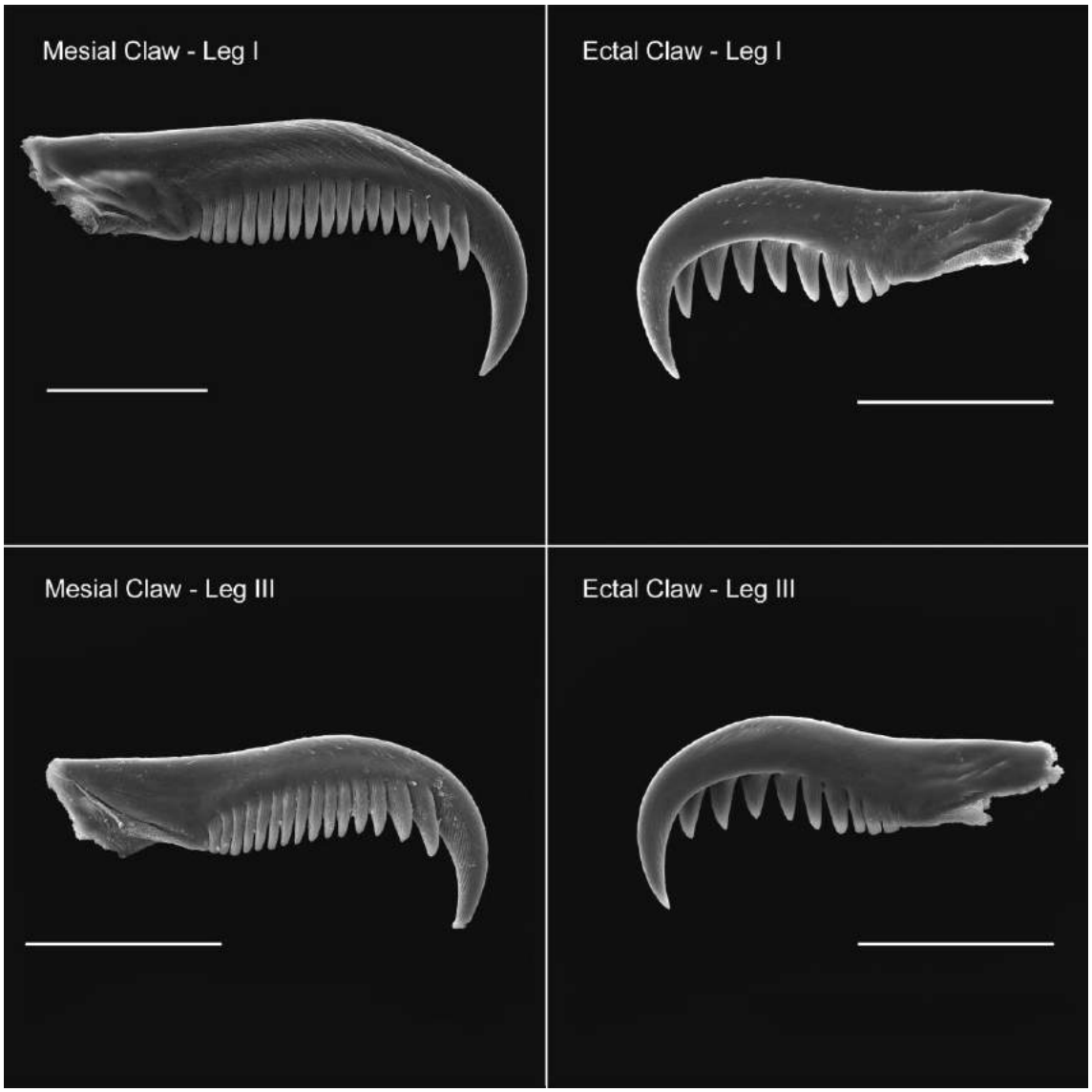

Figure 14. Mesial and ectal claws of leg I and III of *Aphantochilus rogersi* female, representing the general *bauplan* of claws found in Aphantochilinae. White bars below represent 100 µm scale.

APPENDIX 1

Table S1: List of specimens analyzed, including species name, sex, and museum informatio.

internal no.	Museum	Vial no.	Sex	Species
1	IBSP	120875	F	*Acentroscelus albipes*
2	IBSP	120882	F	*Acentroscelus albipes*
3	IBSP	120859	F	*Acentroscelus albipes*
4	UEMG	16296	F	*Acentroscelus albipes*
5	MZSP	27989	F	*Acentroscelus marmoratus*
6	MZSP	27991	F	*Acentroscelus marmoratus*
7	MZSP	27981	F	*Acentroscelus marmoratus*
8	MCTP	17200	F	*Acentroscelus serranus*
9	MCTP	17199	F	*Acentroscelus serranus*
10	MCTP	17194	F	*Acentroscelus serranus*
11	CAS	9046652	F	*Amyceae forticeps*
12	CAS	9046652	F	*Amyceae forticeps*
13	MCTP	1856-1	F	*Aphantochilus rogersi*
14	MCTP	1856-2	F	*Aphantochilus rogersi*
15	MCTP	1856-3	F	*Aphantochilus rogersi*
16	MCTP	1853	F	*Aphantochilus rogersi*
17	MPEG	11407	F	*Aphantochilus rogersi*
18	MCTP	36362	F	*Aphantochilus* sp.
19	KS	15271	F	*Bomis larvata*
20	CAS	9051719	F	*Borboropactus divergens*
21	CAS	9046658	F	*Borboropactus* sp.
22	MPEG	29	F	*Bucranium* sp.
23	MPEG	22617	F	*Bucranium* sp.
24	MPEG	29398	F	*Bucranium* sp.
25	MPEG	14936	F	*Bucranium taurifrons*
26	ZMBH	19617	F	*Cebreeninus annulatus*
27	ZMBH	19617	F	*Cebreeninus annulatus*
28	MCTP	5748	F	*Ceraarachne blanci*
29	MCTP	29951	F	*Ceraarachne blanci*
30	MCTP	6721	F	*Ceraarachne blanci*
31	MCTP	5693	F	*Ceraarachne blanci*
32	AMNH		F	*Coenypha edwardsi*
33	MCZ	133408	F	*Coenypha edwardsi*
34	MCTP	9539	F	*Coenypha edwardsi*
35	ZMUC	11217	F	*Diaea dorsata*
36	SMF	59882-8	F	*Diaea dorsata*
37	SMF	59882-9	F	*Diaea dorsata*
38	MCTP	4082	F	*Epicadus caudatus*
39	MCTP	7593	FJ	*Epicadus caudatus*
40	MCTP	4401	F	*Epicadus caudatus*
41	MCTP	6100	F	*Epicadus caudatus*
42	MCTP	41196	F	*Epicadus heterogaster*
43	MCTP	7101	F	*Epicadus heterogaster*
44	MCTP	41197	F	*Epicadus heterogaster*
45	MCTP	11446	F	*Epicadus heterogaster*
46	MCTP	104	F	*Epicadus heterogaster*
47	MCTP	7106	F	*Epicadus heterogaster*

48	MCTP	21869	F	*Epicadus rubripes*
49	MCTP	33693	F	*Epicadus rubripes*
50	MCTP	21347	F	*Epicadus rubripes*
51	MCTP	39073	F	*Epicadus rubripes*
52	MCTP	39123	F	*Epicadus rubripes*
53	MCTP	34653	F	*Epicadus trituberculatus*
54	MCTP	38706	F	*Epicadus trituberculatus*
55	ZMB	48540	F	*Epidius sp.*
56	ZMB	48541	F	*Epidius sp.*
57	ZMB	48541	F	*Epidius sp.*
58	CAS	9046671-1	F	*Lysiteles major*
59	CAS	9046671-5	F	*Lysiteles major*
60	MCTP	17108	F	*Misumenops pallidus*
61	MCTP	17817	F	*Misumenops pallidus*
62	ZMUC	00001790-1	F	*Misumena vatia*
63	MCTP	42768	F	*Misumenops callinurus*
64	MCTP	1506	F	*Misumenops callinurus*
65	MCTP	28205	F	*Misumenops callinurus*
66	MCTP	40223	F	*Misumenops callinurus*
67	MCTP	28205-N	F	*Misumenops callinurus*
68	MCTP	30398	F	*Misumenops pallens*
69	MCTP	11240	F	*Misumenops pallens*
70	MCTP	1993	F	*Misumenops pallens*
71	MCTP	16653	F	Misumenops pallens
72	MCTP	17104	F	*Misumenops pallidus*
73	MCTP	5495	F	*Onocolus infelix*
74	MCTP	7299	F	*Onocolus infelix*
75	MCTP	5293-1	F	*Onocolus infelix*
76	MCTP	7129	F	*Onocolus intermedius*
77	MCTP	5628	F	*Onocolus intermedius*
78	MCTP	7564	F	*Onocolus intermedius*
79	MCTP	257	F	*Onocolus intermedius*
80	MCTP	4740	F	*Onocolus intermedius*
81	MCTP	1232	F	*Onocolus pentagonos*
82	MCTP	1761-2	F	*Onocolus trifolius*
83	MCTP	1761-4	F	*Onocolus trifolius*
84	MCTP	1761-6	F	*Onocolus trifolius*
85	MCTP	1761-1R	F	*Onocolus trifolius*
86	MCTP	1761-2R	F	*Onocolus trifolius*
87	OUMNH	1268	F	*Phrynarachne ceylonica*
88	OUMNH	1268	F	*Phrynarachne ceylonica*
89	OUMNH	1268	F	*Phrynarachne ceylonica*
90	OUMNH	1268	F	*Phrynarachne ceylonica*
91	CAS	9009578	F	*Pseudoporrhops* sp.
92	MCTP	9918	F	*Runcinia flavida*
93	SMF	60898	F	*Runcinia gramica*
94	MCTP	3493	F	*Sidymella lucida*
95	MCTP	3487	F	*Sidymella lucida*
96	MCTP	21358	F	*Sidymella lucida*
97	MCTP	21356	F	*Sidymella lucida*
98	MCTP	4726	F	*Sidymella lucida*

99	MCTP	37237	F	*Sidymella lucida*
100	MCTP	6045	F	*Sidymella lucida*
101	MCTP	40116	F	*Sidymella lucida*
102	MCTP	41329	F	*Sidymella furcillata*
103	MCTP	7542	F	*Sidymella furcillata*
104	MCTP	5876	F	*Sidymella furcillata*
105	MCTP	8365	F	*Sidymella furcillata*
106	MCTP	42653	F	*Stephanopis parahybana*
107	MCTP	42650	F	*Stephanopis parahybana*
108	MCTP	41973	F	*Stephanopis parahybana*
109	IBSP	46735	F	*Stephanopis parahybana*
110	MCTP	35069	F	*Stephanopis pentacanta*
111	MCTP	10366	F	*Stephanopis pentacanta*
112	MCTP	19435	F	*Stephanopis pentacanta*
113	MNRJ	11515	F	*Stephanopis pentacanta*
114	MCTP	39739	F	*Stephanopoides simoni*
115	MCTP	9504	F	*Stephanopoides simoni*
116	MCTP	9506	F	*Stephanopoides simoni*
117	INPA		F	*Stephanopoides simoni*
118	INPA		F	*Stephanopoides simoni*
119	MCTP	3155-1	F	*Strophius albofaciatus*
120	MCTP	3507	F	*Strophius albofaciatus*
121	MCTP	3155	F	*Strophius albofaciatus*
122	MCTP	43837	F	*Strophius fidelis*
123	MCTP	34480	F	*Strophius fidelis*
124	IBSP	37607	F	*Strophius nigricans*
125	MCTP	11148	F	*Strophius nigricans*
126	OUMNH	5033-1	F	*Synema globosa*
127	OUMNH	5033-2	F	*Synema globosa*
128	OUMNH	5033-3	F	*Synema globosa*
129	ZMBH	80793-N8	F	*Synema globosa*
130	SMF	29347	F	*Thomisus onostus*
131	SMF	1805	F	*Thomisus onostus*
132	MPEG	5414	F	*Titidius galbanatus*
133	MCTP	1449	F	*Titidius galbanatus*
134	INPA		F	*Titidius galbanatus*
135	IBSP	9486	F	*Titidius galbanatus*
136	MPEG	4404	F	*Tmarus litoralis*
137	MCTP	40707	F	*Tmarus litoralis*
138	MCTP	28419	F	*Tmarus polyandrus*
139	MCTP	10241	F	*Tmarus polyandrus*
140	MCTP	11667	F	*Tmarus polyandrus*
141	MCTP	21364	F	*Tmarus polyandrus*
142	IZMBH	9016	F	*Xysticus acerbus*
143	SMF	3755-3	F	*Xysticus audax*
144	SMF	3755-5	F	*Xysticus audax*
145	MZSP	2787	M	*Acentroscelus marmoratus*
146	MZSP	27979	M	*Acentroscelus marmoratus*
147	MZSP	27499	M	*Acentroscelus marmoratus*
148	MCTP	10746	M	*Acentroscelus serranus*
149	MCN	24414	M	*Acentroscelus serranus*

150	MCN	24414	M	*Acentroscelus serranus*
151	CAS	9033827	M	*Borboropactus bituberculatus*
152	CAS	9046658	M	*Borboropactus* sp.
154	MPEG	22620	M	*Bucranium* sp.
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160	MPEG	14948	M	*Bucranium taurifrons*
161	MCTP	5748	M	*Ceraarachne blanci*
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163	MCTP	16597	M	*Ceraarachne blanci*
164	MCTP	5693	M	*Ceraarachne blanci*
165	CAS	9072303	M	*Coenypha edwardsi*
166	MCZ	133409	M	*Coenypha edwardsi*
167	AMNH		M	*Coenypha edwardsi*
168	ZMUC	6114	M	*Diaea dorsata*
169	SMF	59882-10	M	*Diaea dorsata*
170	SMF	59882-11	M	*Diaea dorsata*
171	MCTP	365	M	*Epicadus caudatus*
172	MCTP	10470	M	*Epicadus caudatus*
173	MCTP	7524	M	*Epicadus caudatus*
174	MCTP	240	M	*Epicadus caudatus*
175	MCTP	10246	M	*Epicadus caudatus*
176	MCTP	32096	M	*Epicadus heterogaster*
177	MCTP	1772	M	*Epicadus heterogaster*
178	MCTP	527	M	*Epicadus rubripes*
179	MCTP	2855	M	*Epicadus rubripes*
180	MCTP	5432	M	*Epicadus rubripes*
181	MCTP	37281	M	*Epicadus rubripes*
182	MCTP	10313	M	*Epicadus trituberculatus*
183	MCTP	2482	M	*Epicadus trituberculatus*
184	ZMB	48541	M	*Epidius* sp.
185	ZMB	48541	M	*Epidius* sp.
186	ZMB	48541	M	*Epidius* \.
187	CAS	9046671-2	M	*Lysiteles major*
188	CAS	9046671-3	M	*Lysiteles major*
189	MCTP	18159	M	*Misumenops pallidus*
190	MCTP	30355	M	*Misumenops pallidus*
191	ZMUC	6101	M	*Misumena vatia*
192	MCTP	41374	M	*Misumenops pallens*
193	MCTP	41369	M	*Misumenops pallens*
194	MCTP	12292	M	*Misumenops pallens*
195	MCTP	11397	M	*Misumenops pallens*
196	MCTP	39657	M	*Misumenops pallidus*
197	MCTP	41199	M	*Onocolus garrunchus*
198	MCTP	30590	M	*Onocolus infelix*
199	MCTP	8098	M	*Onocolus infelix*
200	MCTP	36824	M	*Onocolus intermedius*
201	MCTP	31892	M	*Onocolus intermedius*

202	MCTP	366	M	*Onocolus intermedius*
203	MCTP	34629	M	*Onocolus intermedius*
204	MCTP	5241	M	*Onocolus intermedius*
205	MCTP	1441	M	*Onocolus pentagnos*
206	MCTP	1761-1	M	*Onocolus trifolius*
207	MCTP	1761-3	M	*Onocolus trifolius*
208	MCTP	1761-1R	M	*Onocolus trifolius*
209	MCTP	1761-2R	M	*Onocolus trifolius*
210	CAS	9010108	M	*Pseudoporrhops sp.*
211	MCTP	9918	M	*Runcinia flavida*
212	SMF	60898	M	*Runcinia gramica*
213	MCTP	3487	M	*Sidymella lucida*
214	MCTP	12334	M	*Sidymella lucida*
215	MCTP	8247	M	*Sidymella furcillata*
216	MCTP	41968	M	*Stephanopis parahybana*
217	MCTP	41967	M	*Stephanopis parahybana*
218	MCTP	31973	M	*Stephanopis parahybana*
219	MCTP	6982	M	*Stephanopis pentacanta*
220	MCTP	10366	M	*Stephanopis pentacanta*
221	MCTP	40117	M	*Stephanopis pentacanta*
222	MNRJ	11534	M	*Stephanopis pentacanta*
223	INPA		M	*Stephanopoides simoni*
224	MCTP	6719	M	*Strophius albofaciatus*
225	MCTP	7387	M	*Strophius albofaciatus*
226	MCTP	3522	M	*Strophius albofaciatus*
227	MCTP	43837	M	*Strophius fidelis*
228	MZSP	49784	M	*Strophius fidelis*
229	UFMG	11001	M	*Strophius fidelis*
230	MCTP	3017	M	*Strophius nigricans*
231	MCTP	43835-1	M	*Strophius nigricans*
232	MCTP	43835-2	M	*Strophius nigricans*
233	OUMNH	1272-1	M	*Synema globosa*
234	OUMNH	1272-2	M	*Synema globosa*
235	OUMNH	1272-3	M	*Synema globosa*
236	SMF	29347	M	*Thomisus onostus*
237	SMF	1805	M	*Thomisus onostus*
238	MPEG	15547	M	*Titidius galbanatus*
239	MCTP	1449	M	*Titidius galbanatus*
240	MCTP	3965	M	*Titidius galbanatus*
241	MCTP	31964	M	*Titidius galbanatus*
242	MPEG	5459	M	*Tmarus litoralis*
243	MCTP	40710	M	*Tmarus litoralis*
244	MCTP	36455	M	*Tmarus polyandrus*
245	MCTP	21690-1	M	*Tmarus polyandrus*
246	MCTP	21690-2	M	*Tmarus polyandrus*
247	MCTP	21364	M	*Tmarus polyandrus*
248	IZMBH	14126	M	*Xysticus acerbus*
249	SMF	3755-2	M	*Xysticus audax*
250	SMF	3755-1	M	*Xysticus audax*

APPENDIX 2

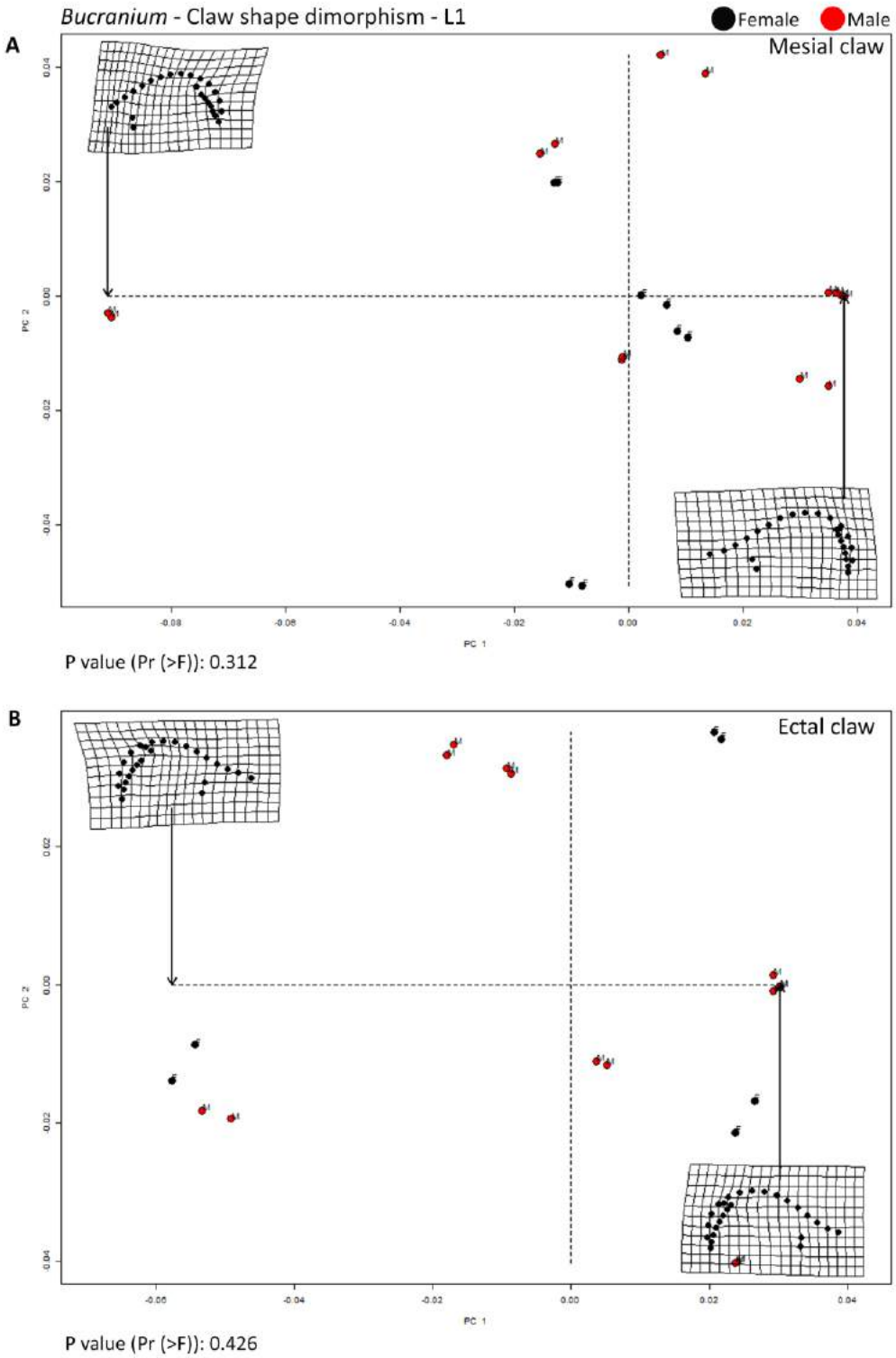
Referred bibliography for habitat assignment. For more details access the link <www.encurtador.com.br/iqC38>.

APPENDIX 3

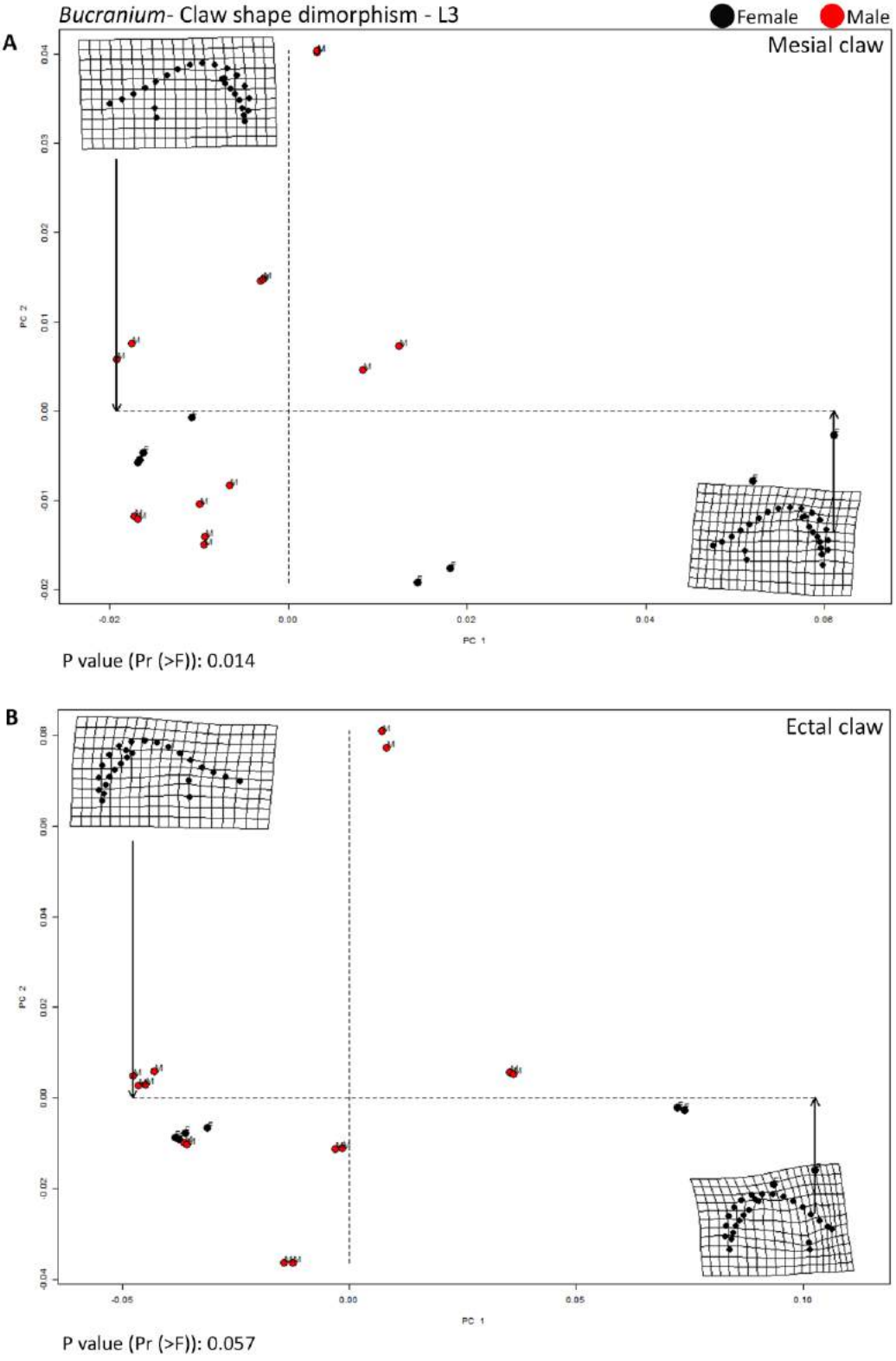
Tables representing the p-value of MANOVA pairwise comparisons for each claw of each leg, in male and females separately. Significant p-values ($p \leq 0.05$) are highlighted in green. <www.encurtador.com.br/iqC38>

APPENDIX 4

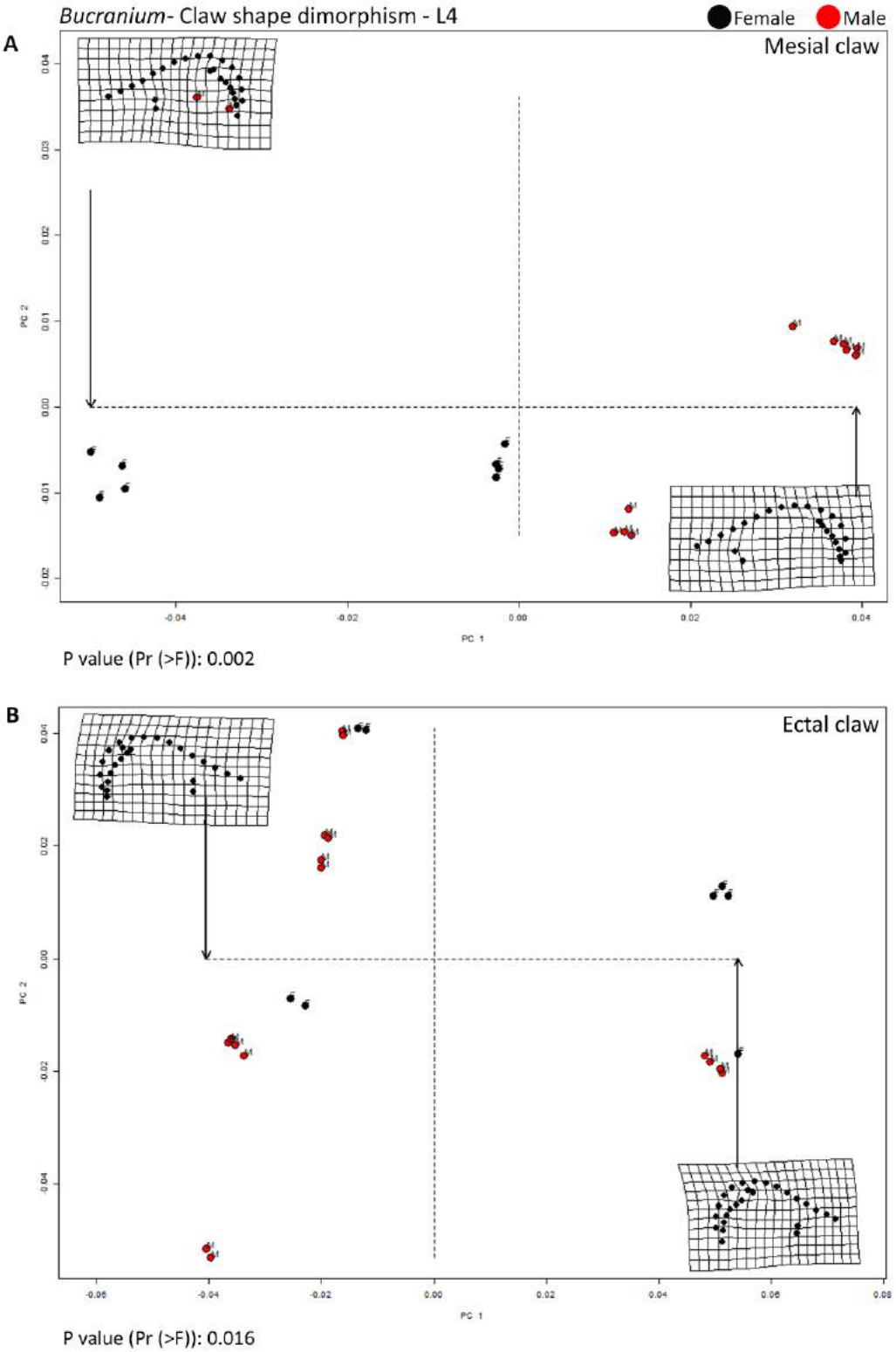
Principal Component Analysis and p-values of MANOVA testing sexual dimorphism in each claw of each leg in each analyzed genus.



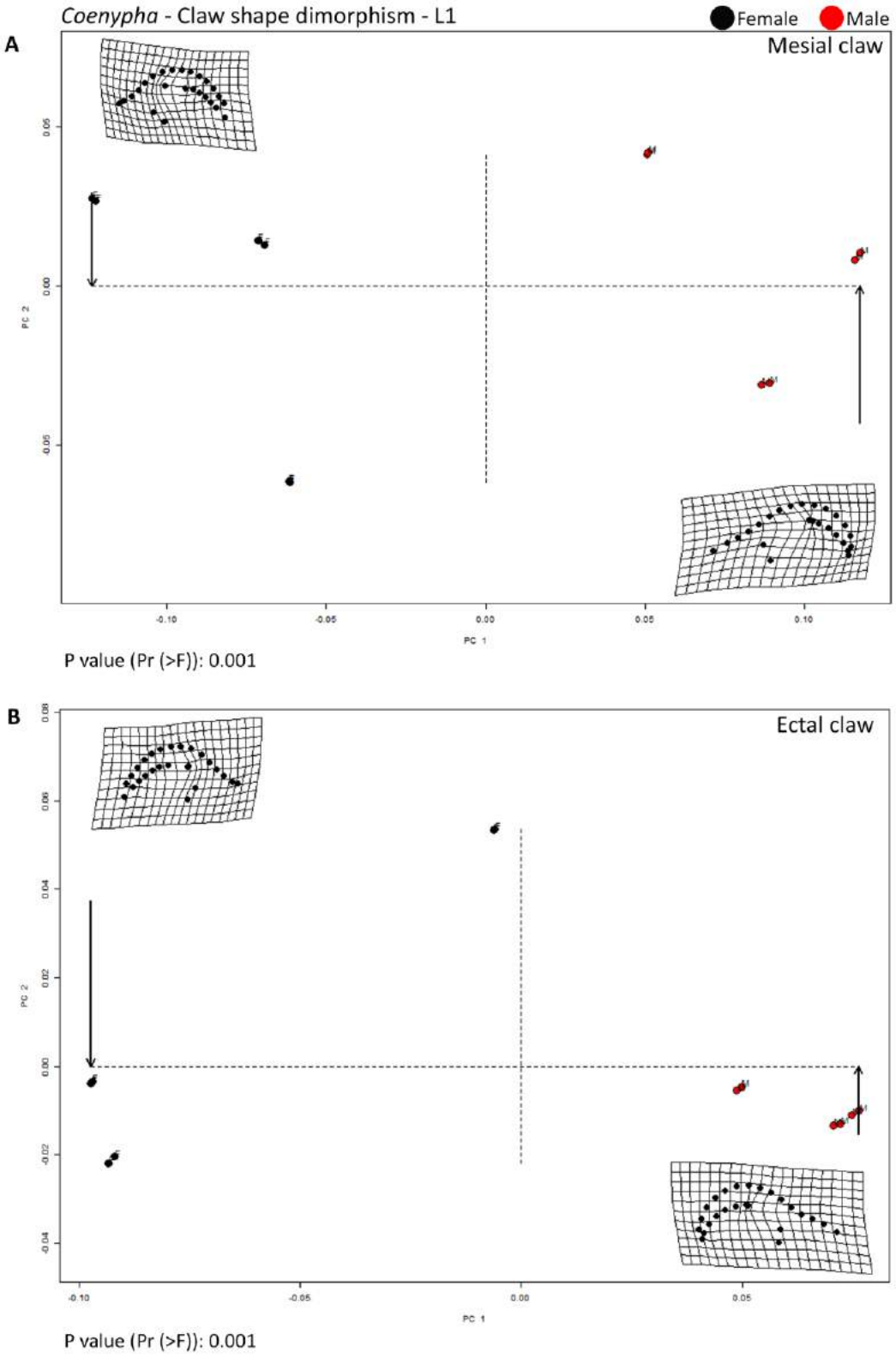
Graphic 1. Principal components analysis showing claws' variation in leg I between males and females of *Bucranium* p-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



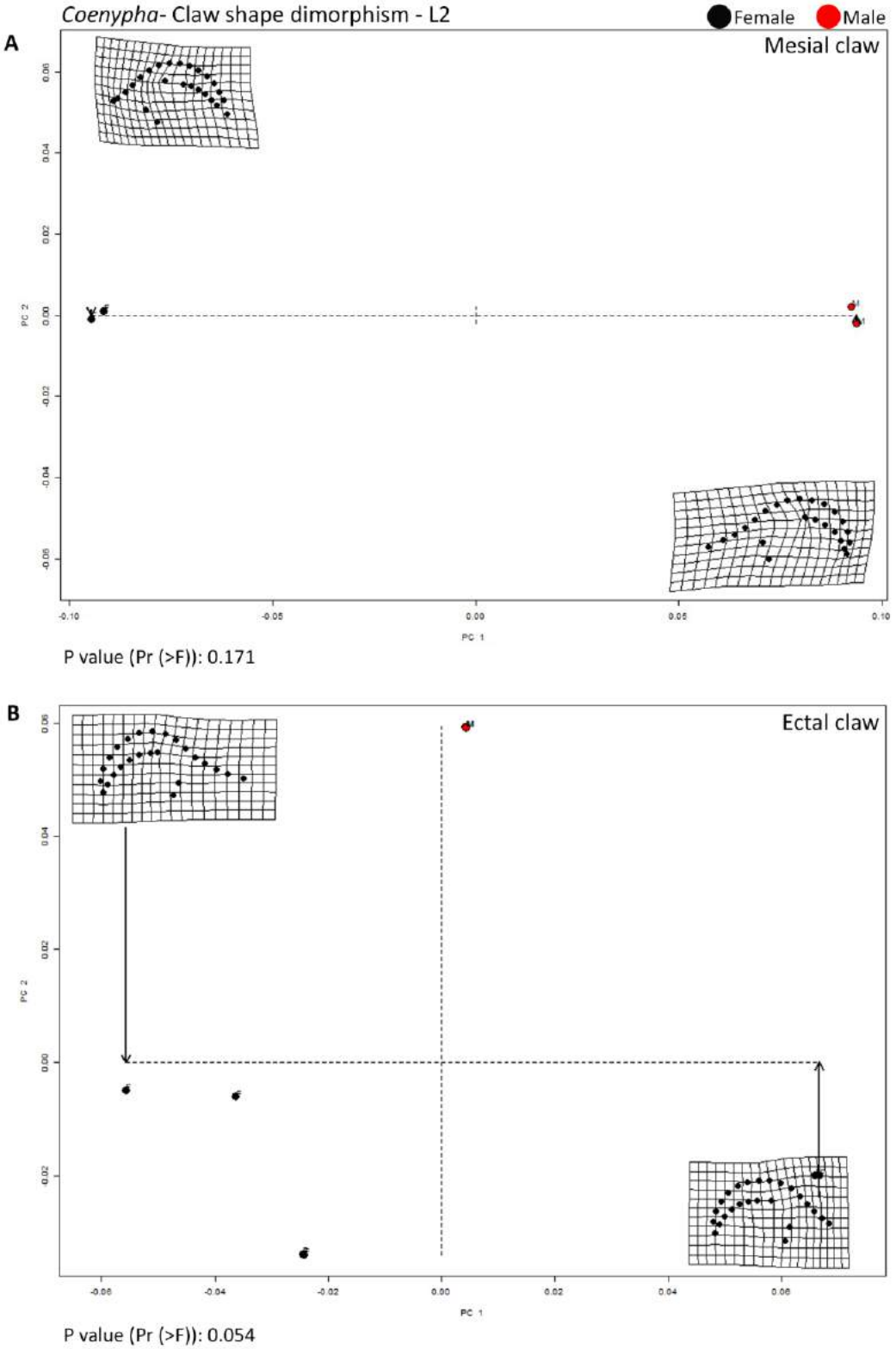
Graphic 2. Principal components analysis showing claws' variation in leg III between males and females of Bucranium p-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



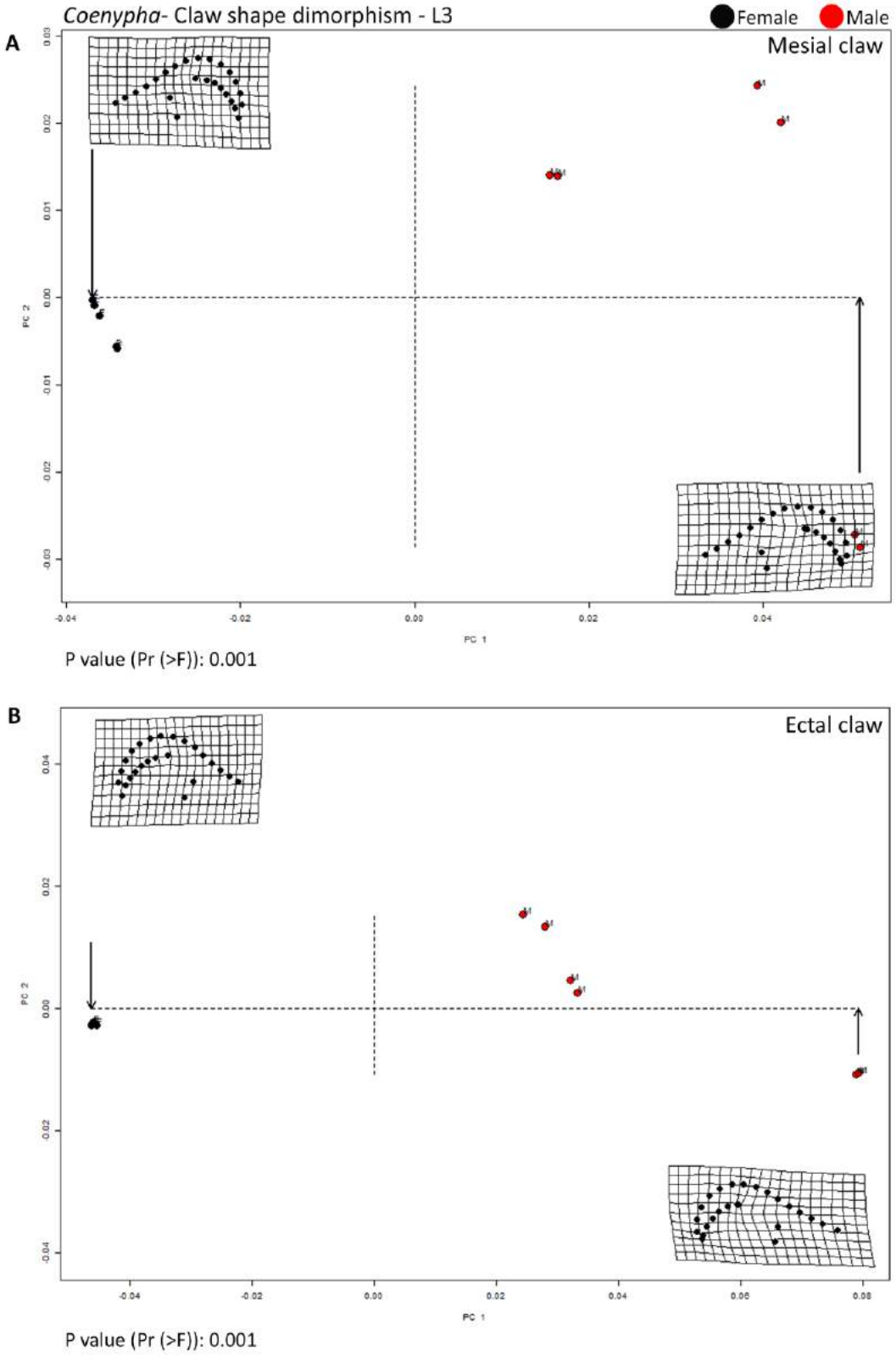
Graphic 3. Principal components analysis showing claws' variation in leg IV between males and females of *Bucranium* p-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



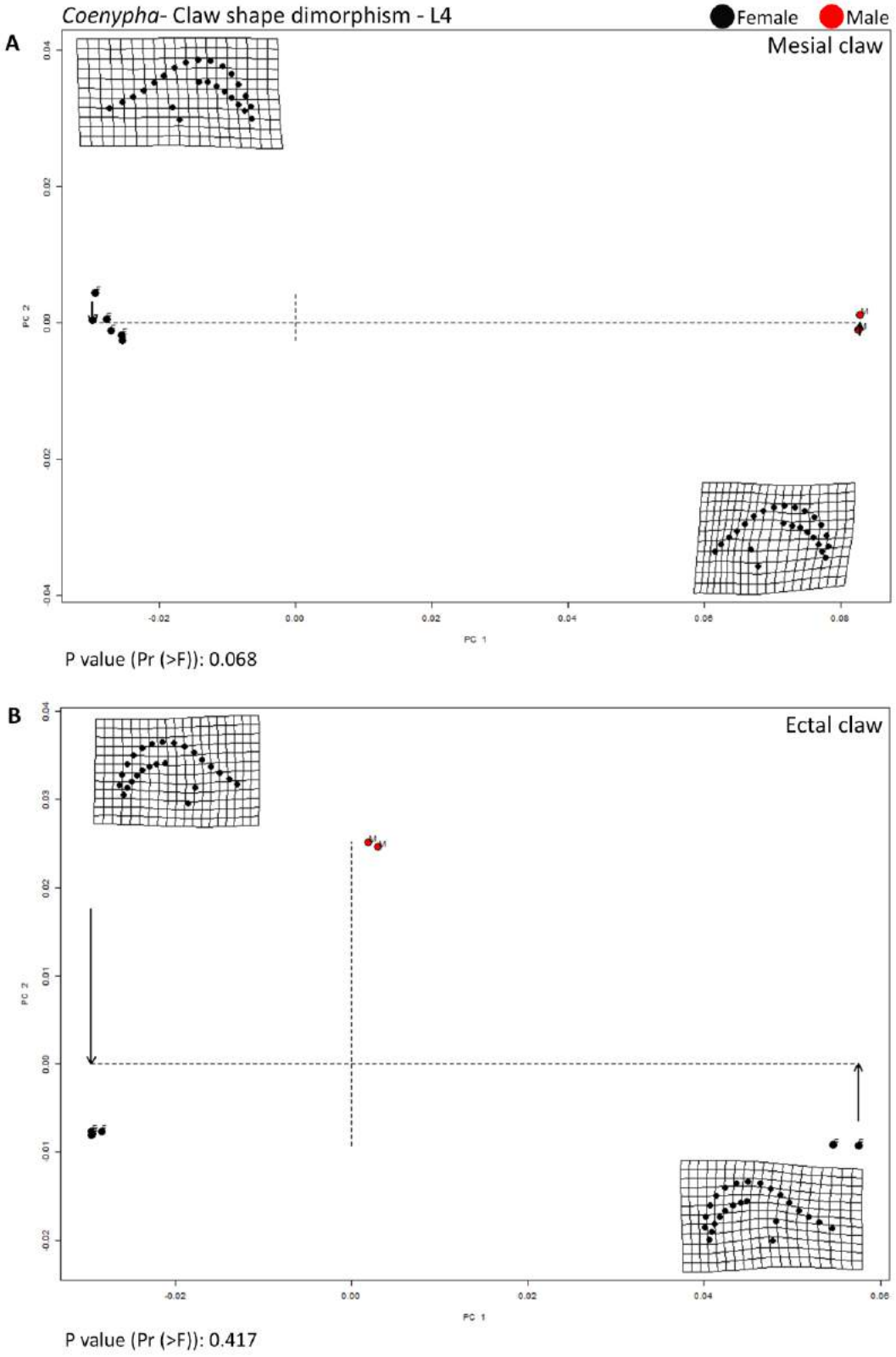
Graphic 4. Principal components analysis showing claws' variation in leg I between males and females of *Coenypha*. P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



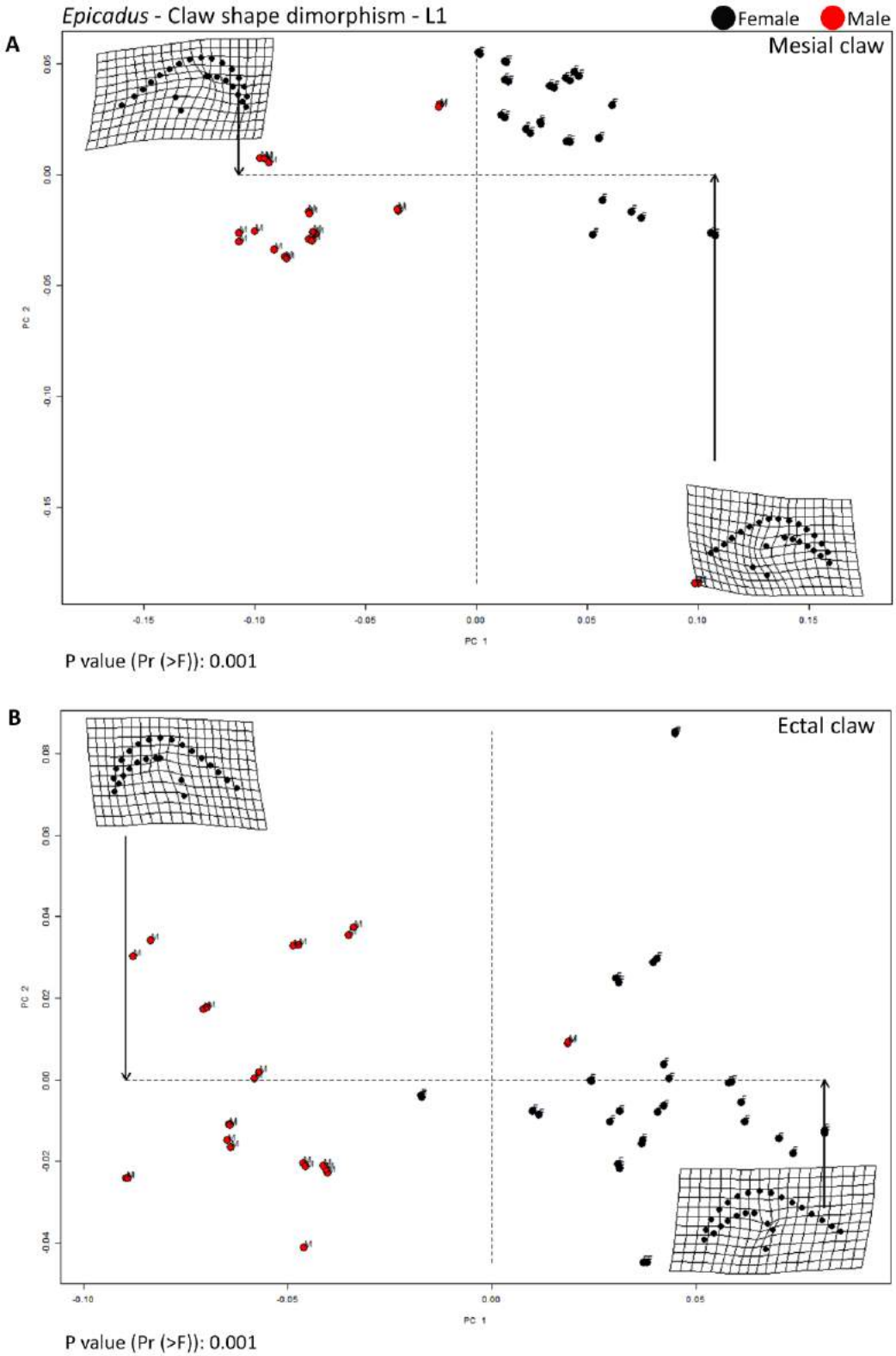
Graphic 5. Principal components analysis showing claws' variation in leg II between males and females of *Coenypha.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



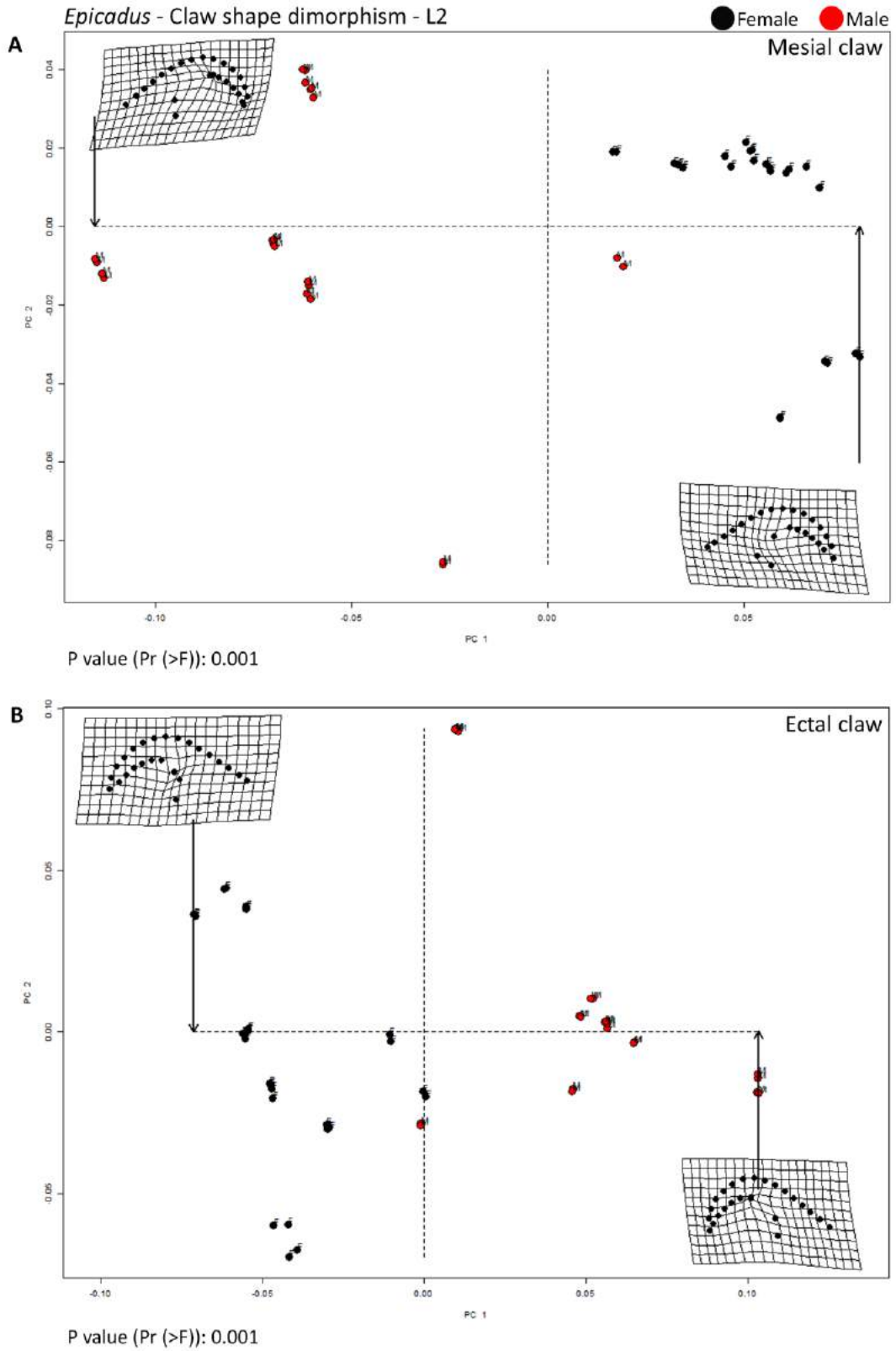
Graphic 6. Principal components analysis showing claws' variation in leg III between males and females of *Coenypha.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



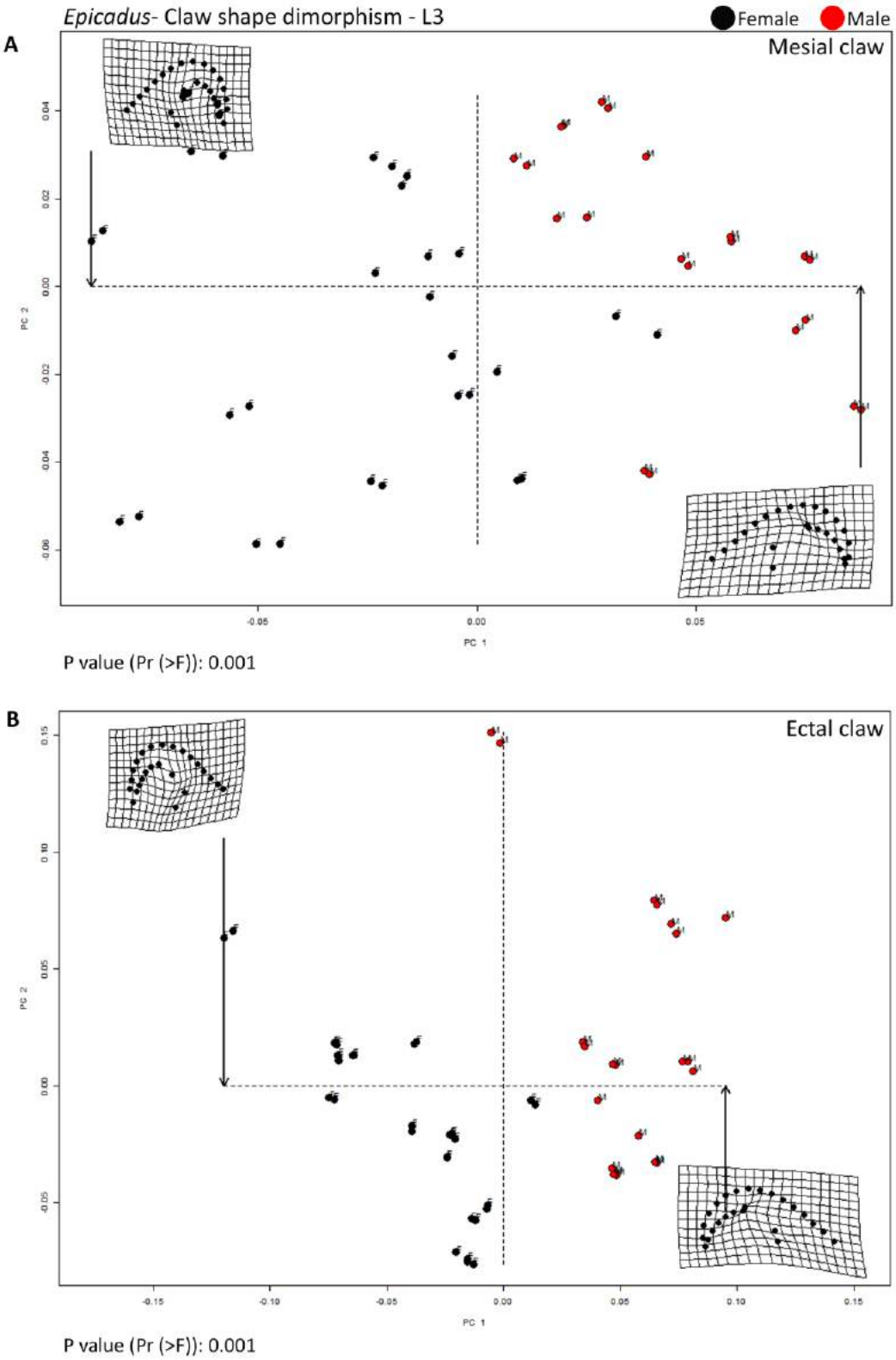
Graphic 7. Principal components analysis showing claws' variation in leg IV between males and females of *Coenypha.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



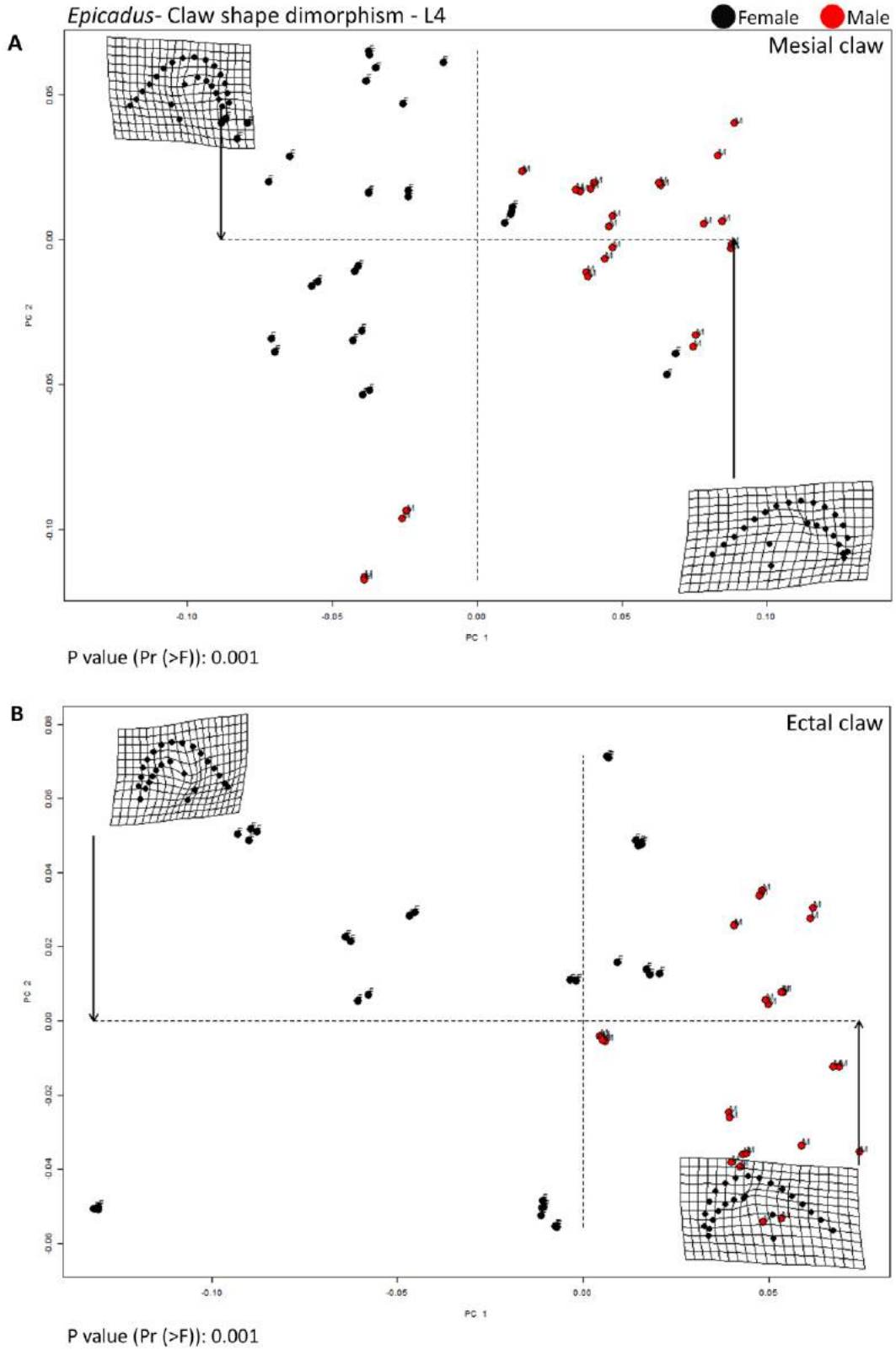
Graphic 8. Principal components analysis showing claws' variation in leg I between males and females of *Epicadus.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively.



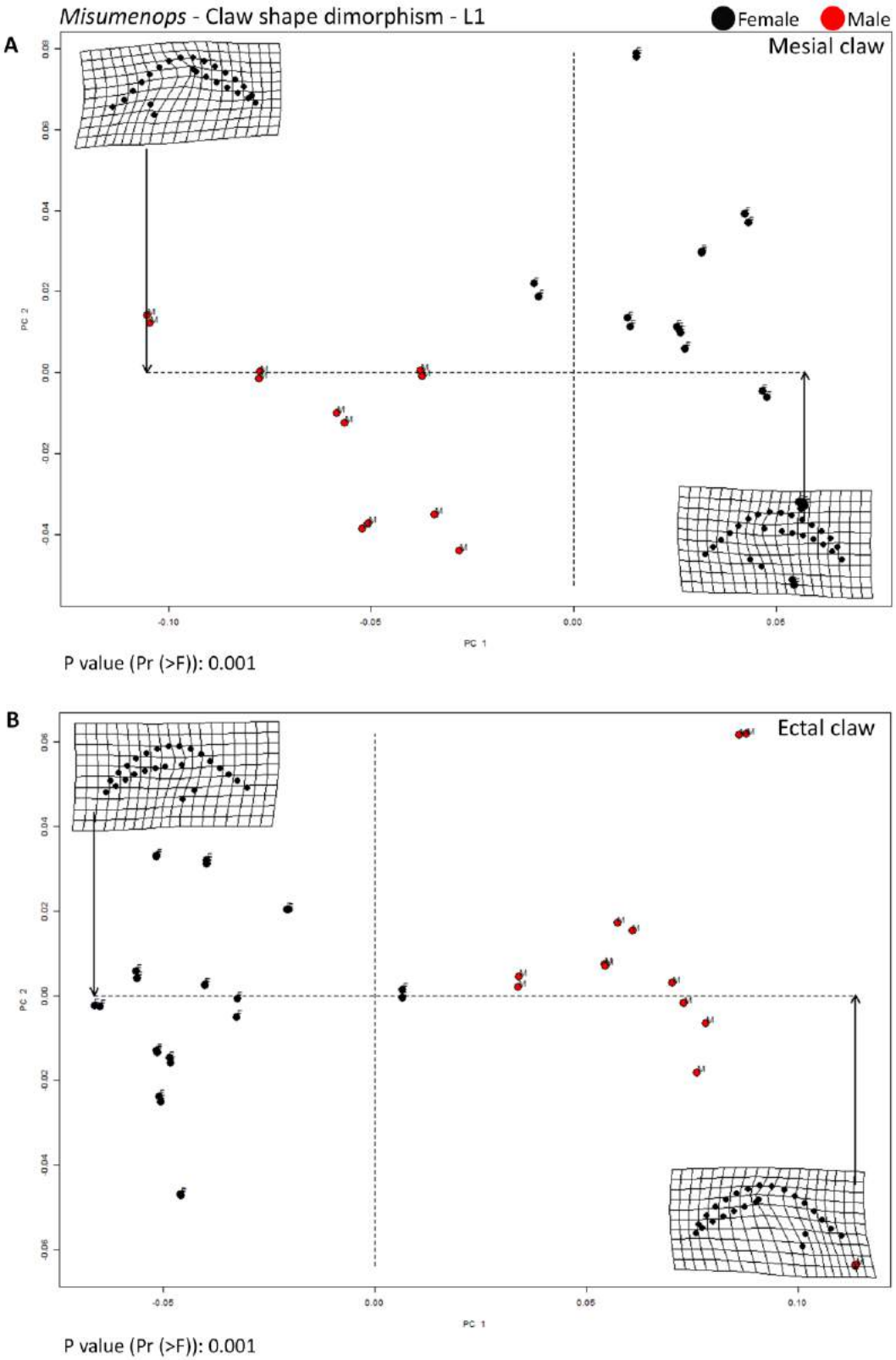
Graphic 9. Principal components analysis showing claws' variation in leg II between males and females of *Epicadus.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



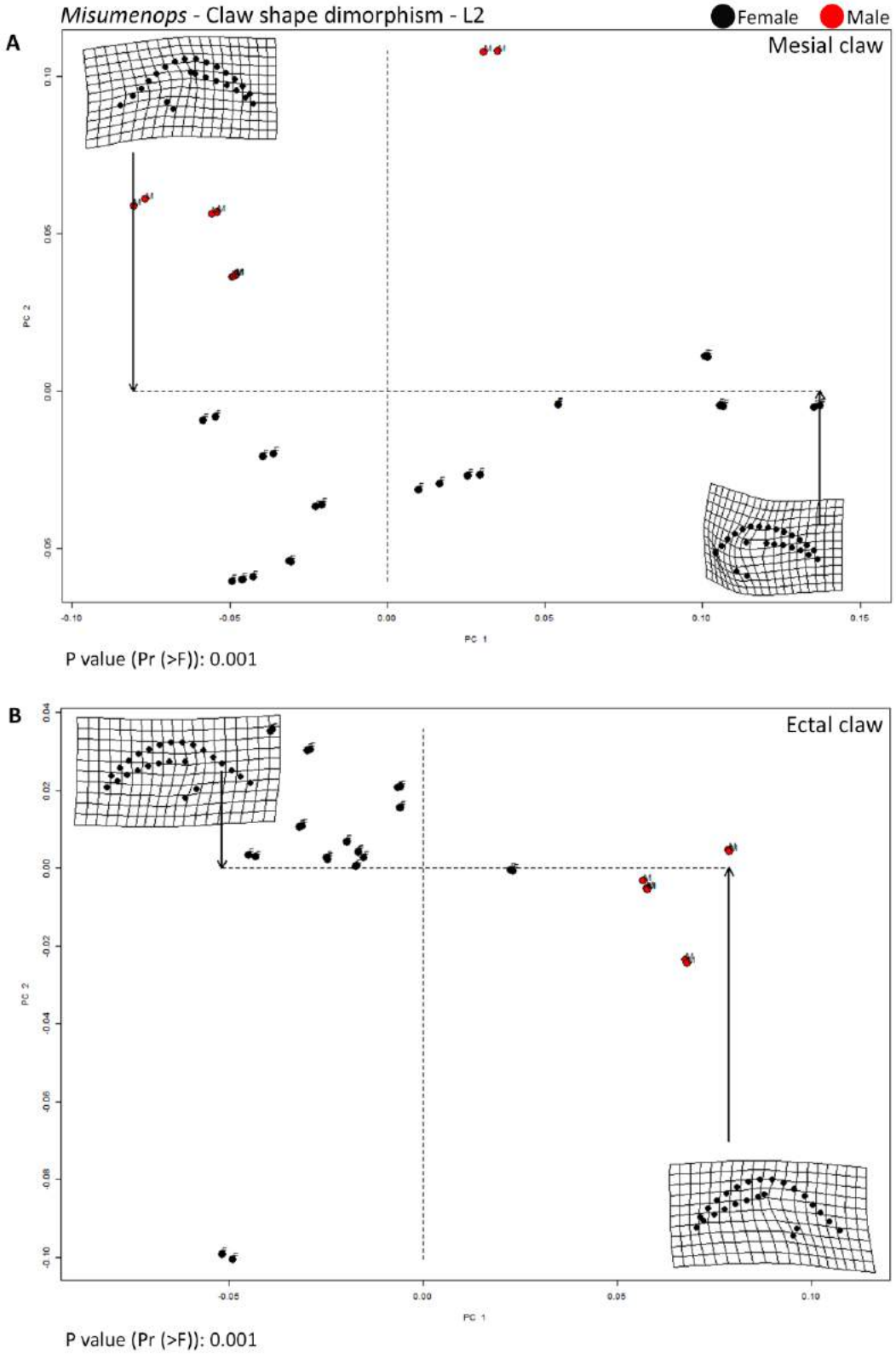
Graphic 10. Principal components analysis showing claws' variation in leg III between males and females of *Epicadus.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



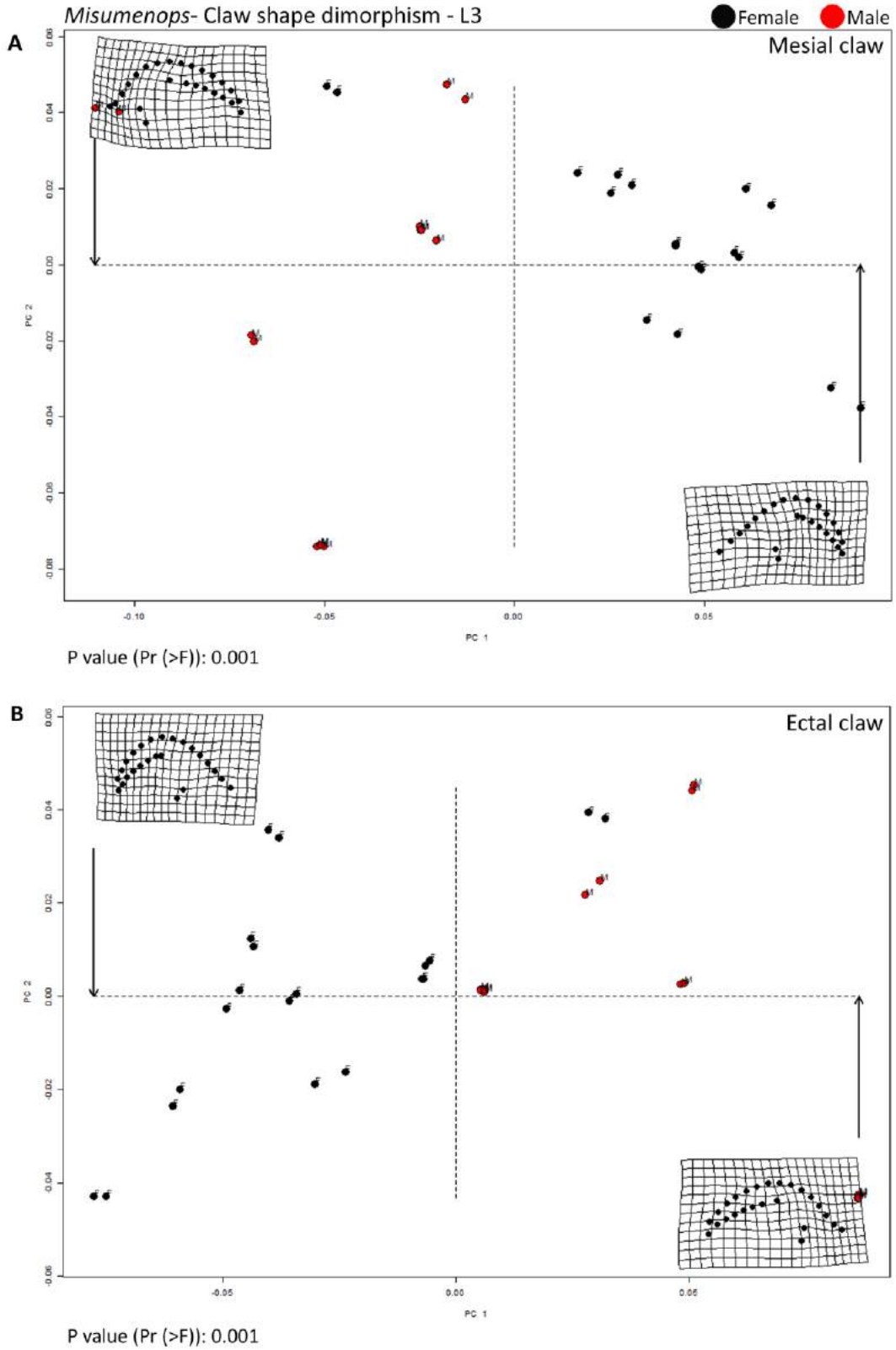
Graphic 11. Principal components analysis showing claws' variation in leg IV between males and females of *Epicadus.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



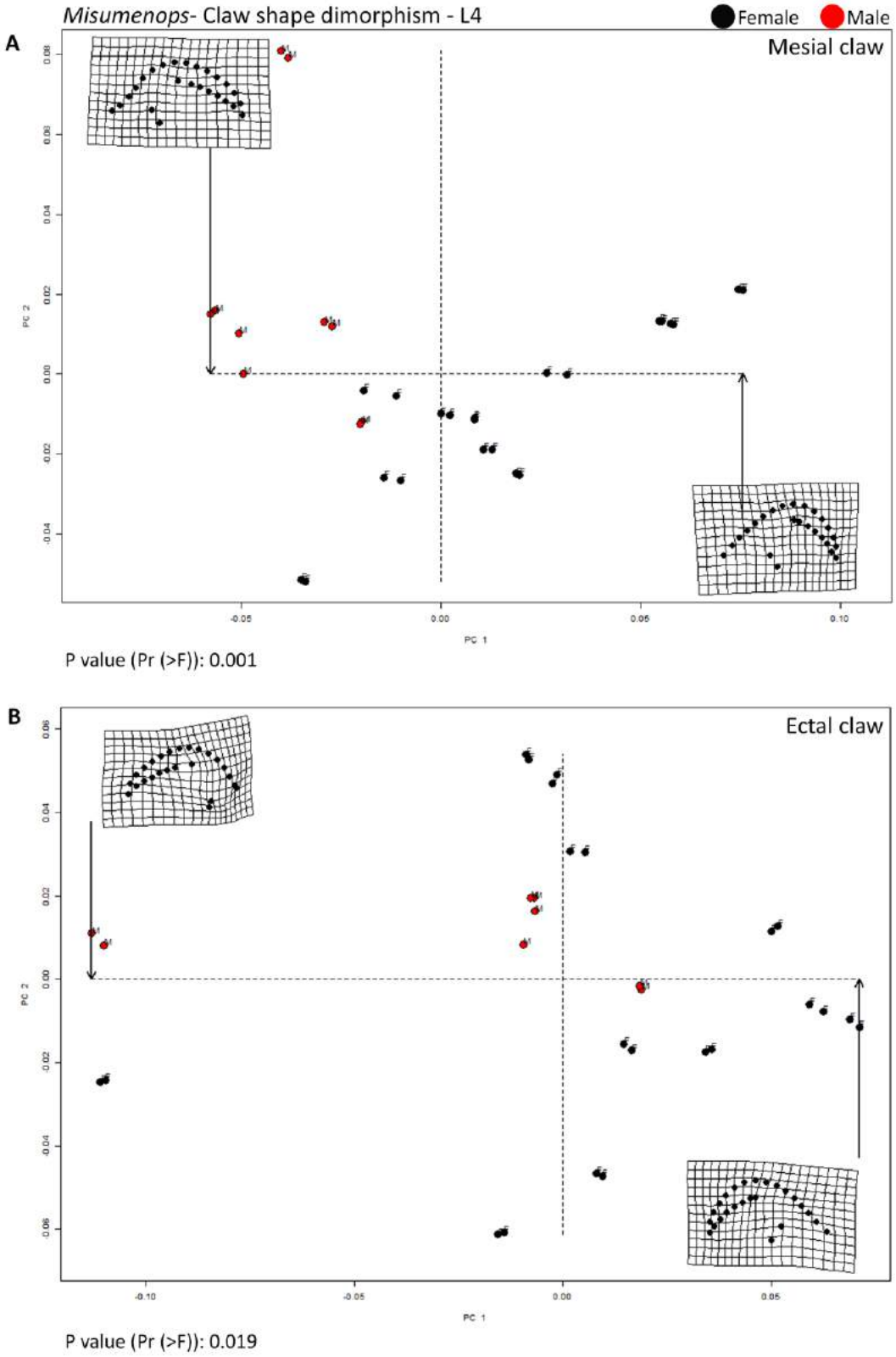
Graphic 12. Principal components analysis showing claws' variation in leg I between males and females of *Misumenops.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively.



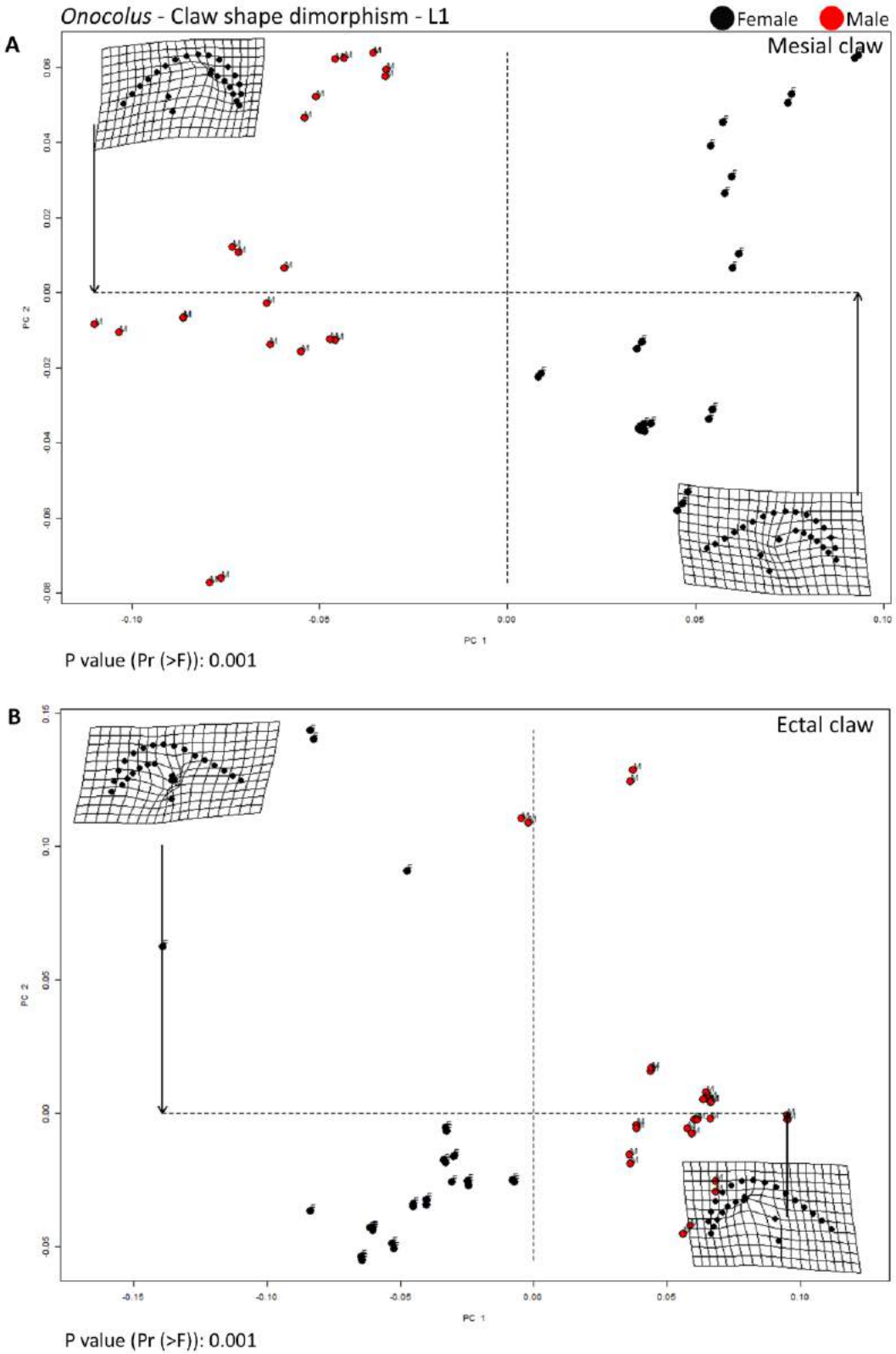
Graphic 13. Principal components analysis showing claws' variation in leg II between males and females of *Misumenops.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



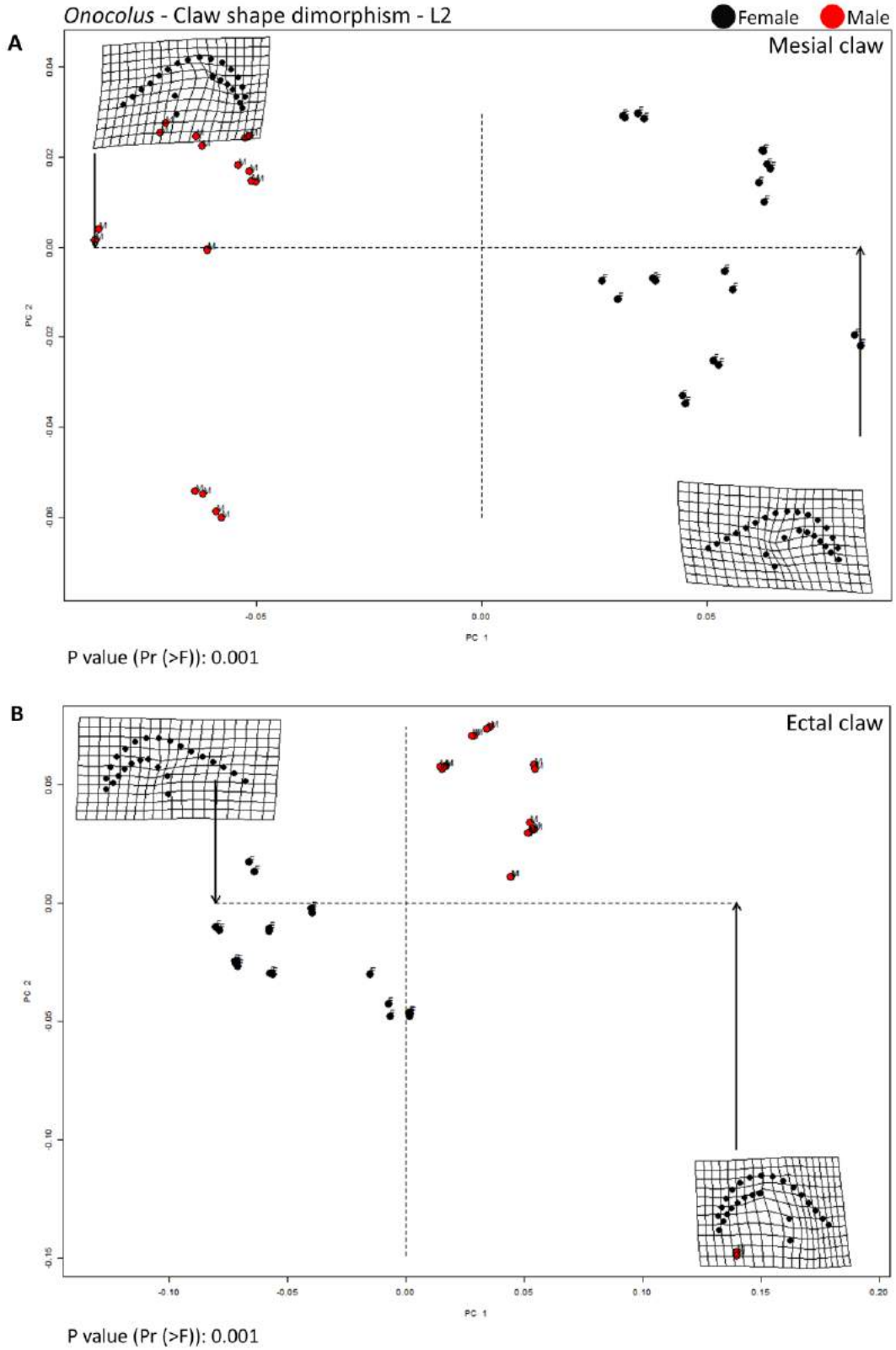
Graphic 14. Principal components analysis showing claws' variation in leg III between males and females of *Misumenops.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



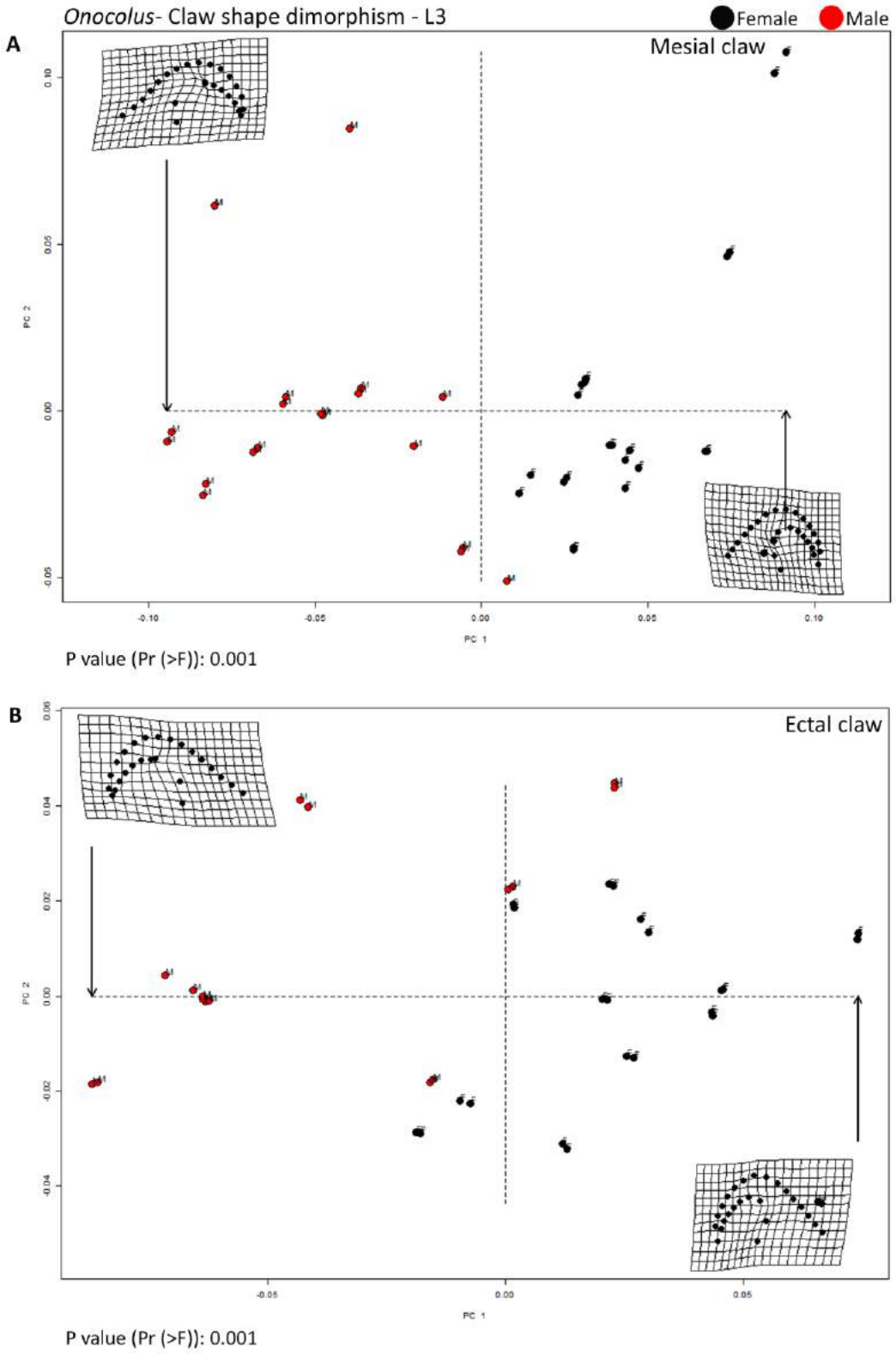
Graphic 15. Principal components analysis showing claws' variation in leg IV between males and females of *Misumenops.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively.



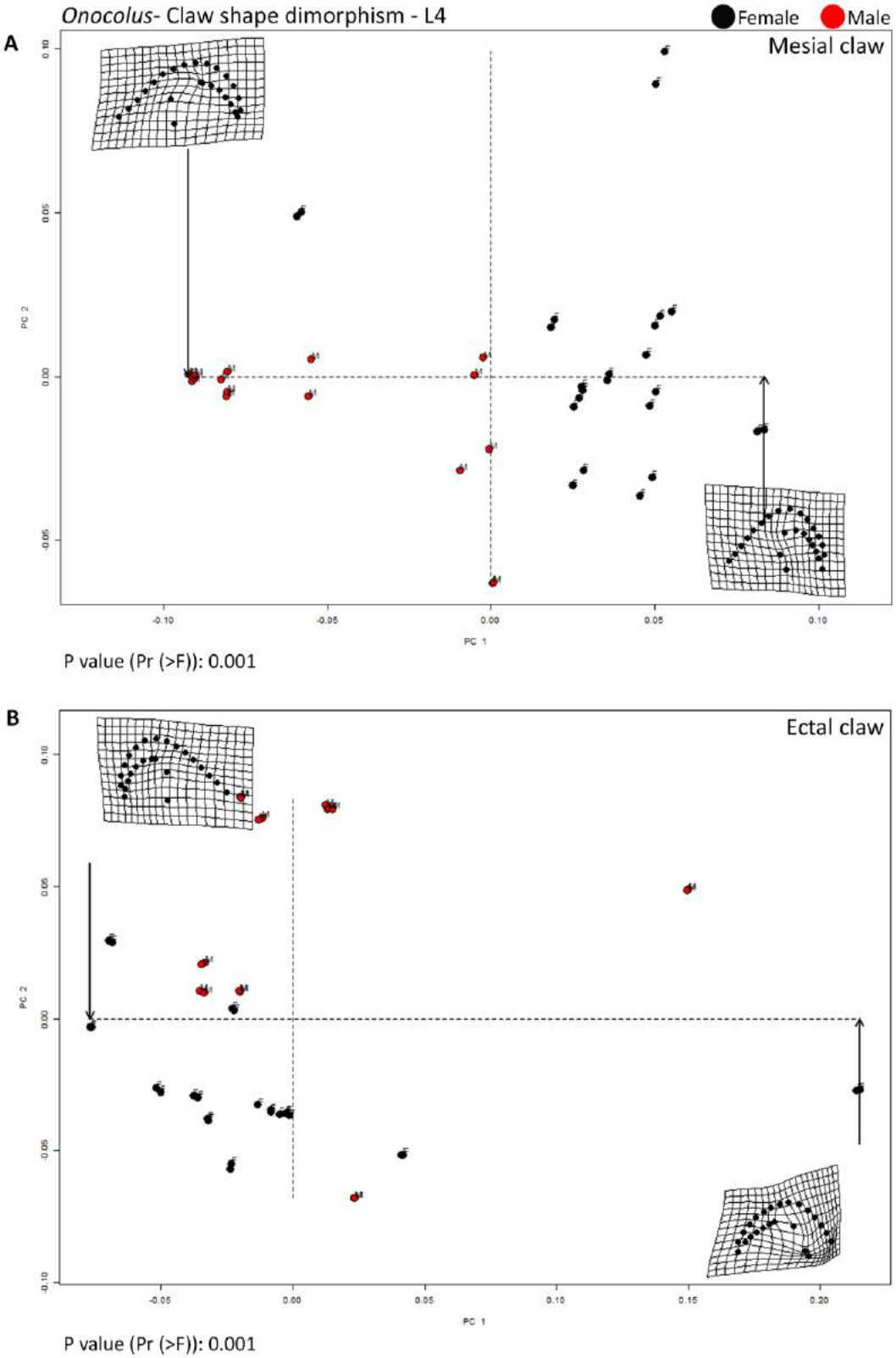
Graphic 16. Principal components analysis showing claws' variation in leg I between males and females of *Onocolus.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



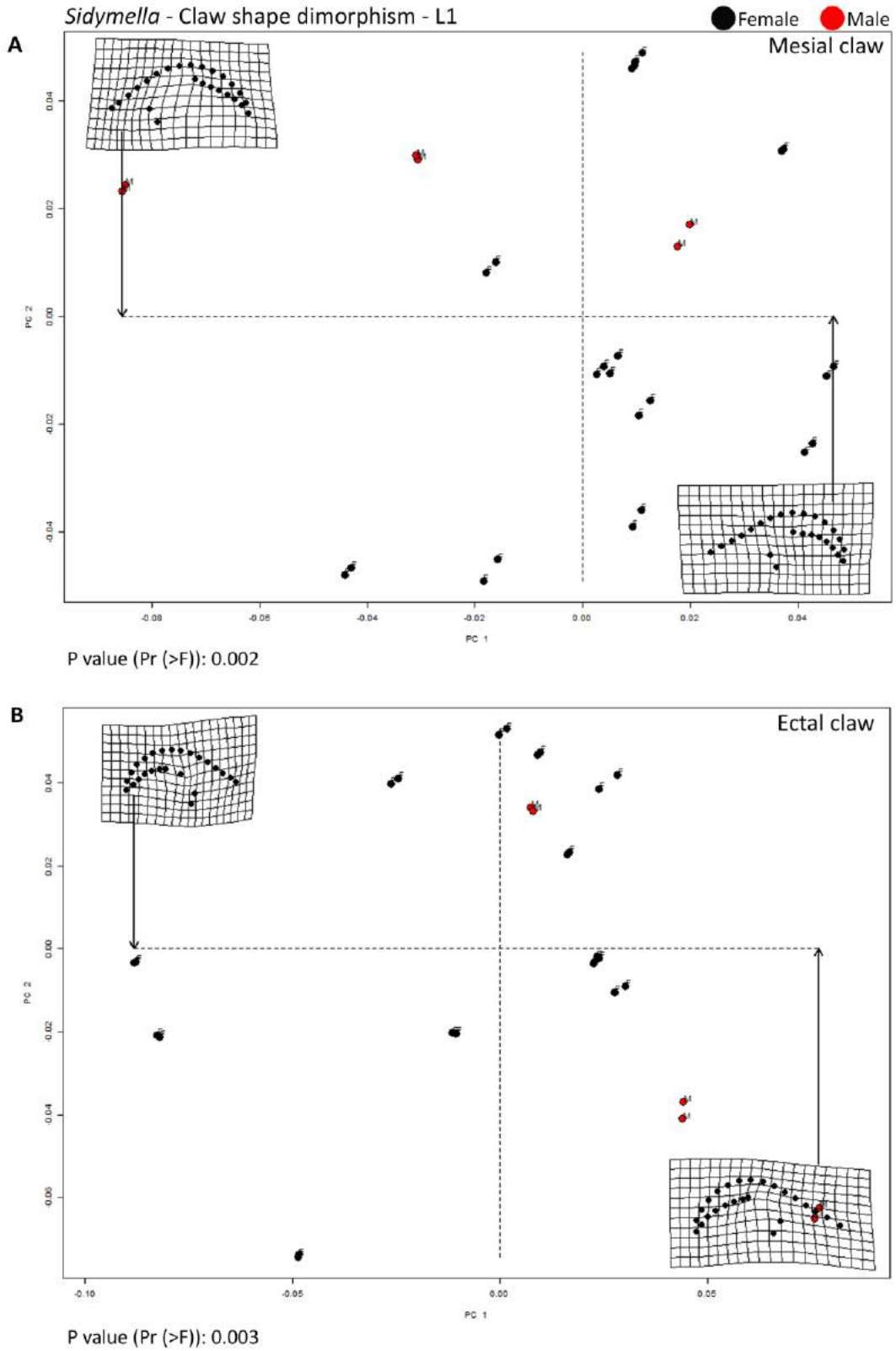
Graphic 17. Principal components analysis showing claws' variation in leg II between males and females of *Onocolus.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively.



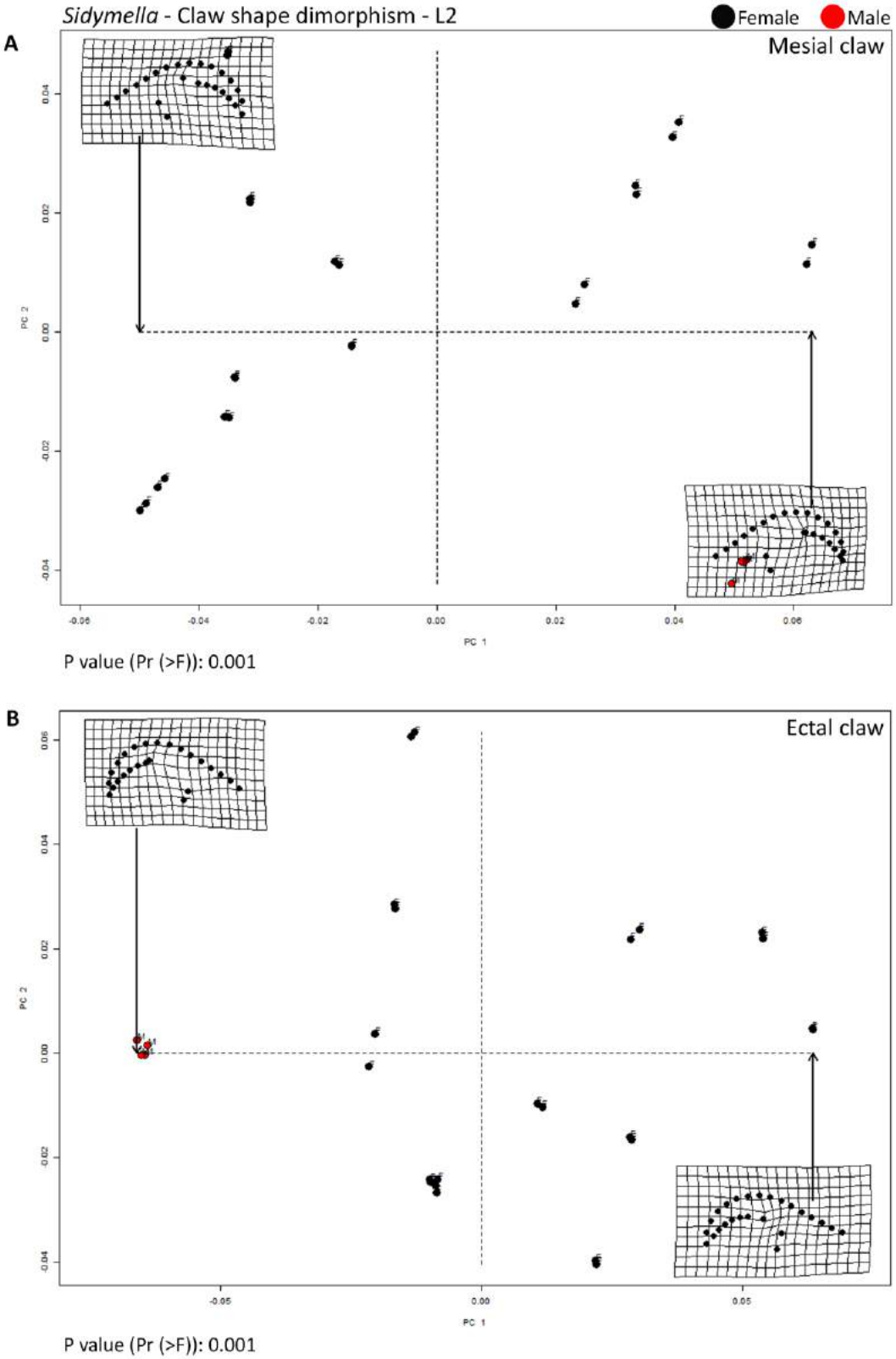
Graphic 18. Principal components analysis showing claws' variation in leg III between males and females of *Onocolus.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively.



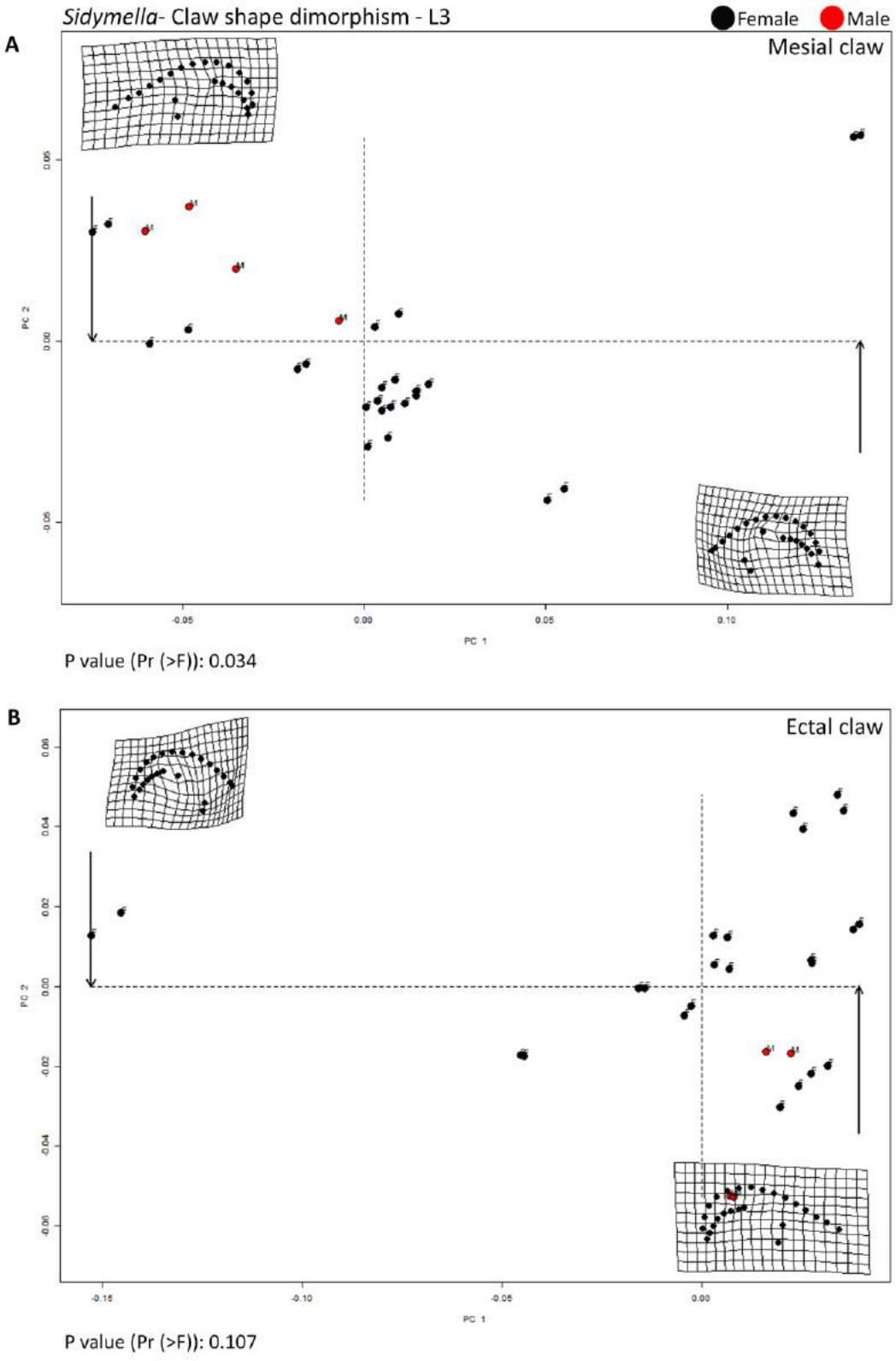
Graphic 19. Principal components analysis showing claws' variation in leg IV between males and females of *Onocolus.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



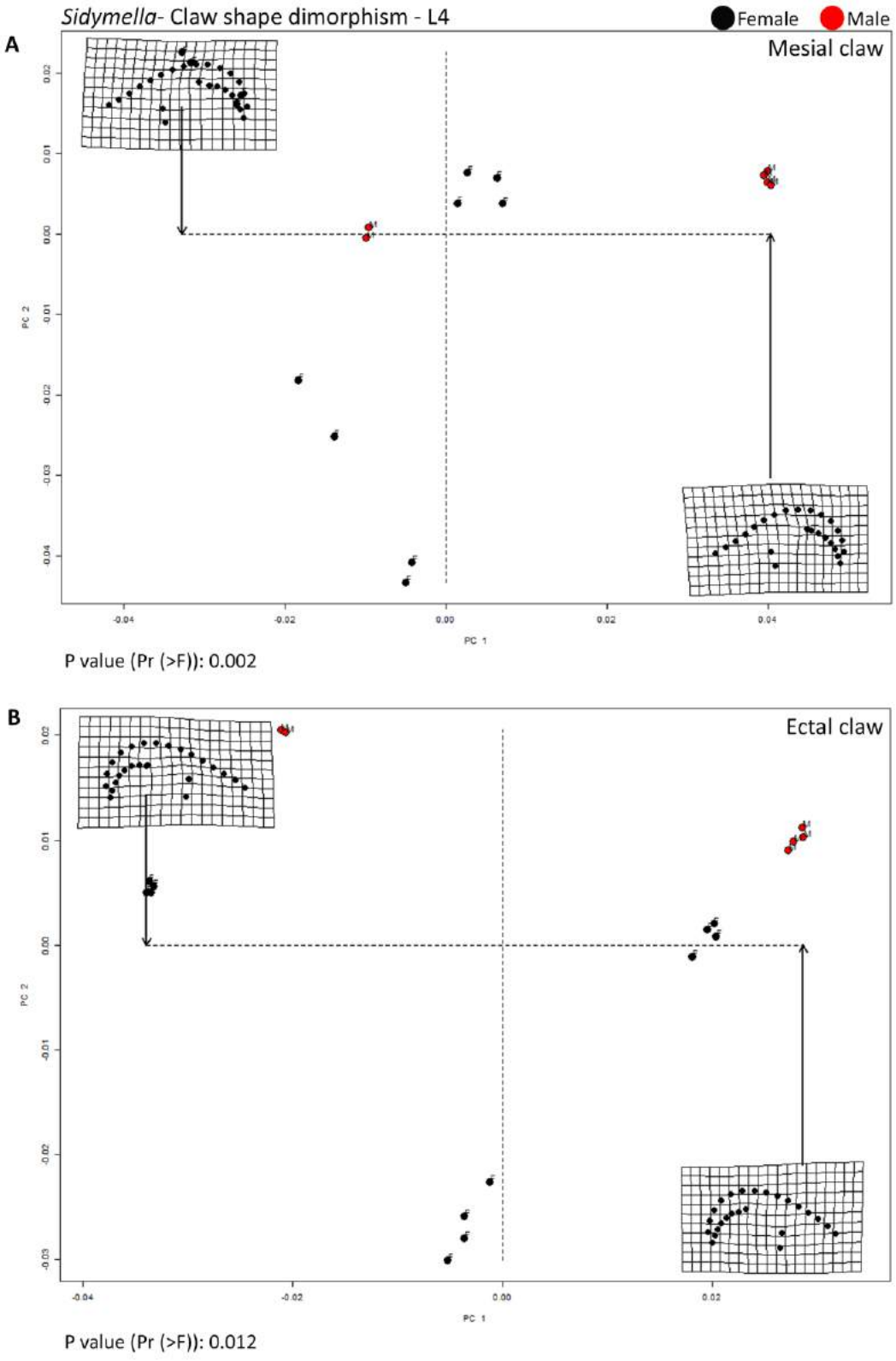
Graphic 20. Principal components analysis showing claws' variation in leg I between males and females of *Sidymella.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



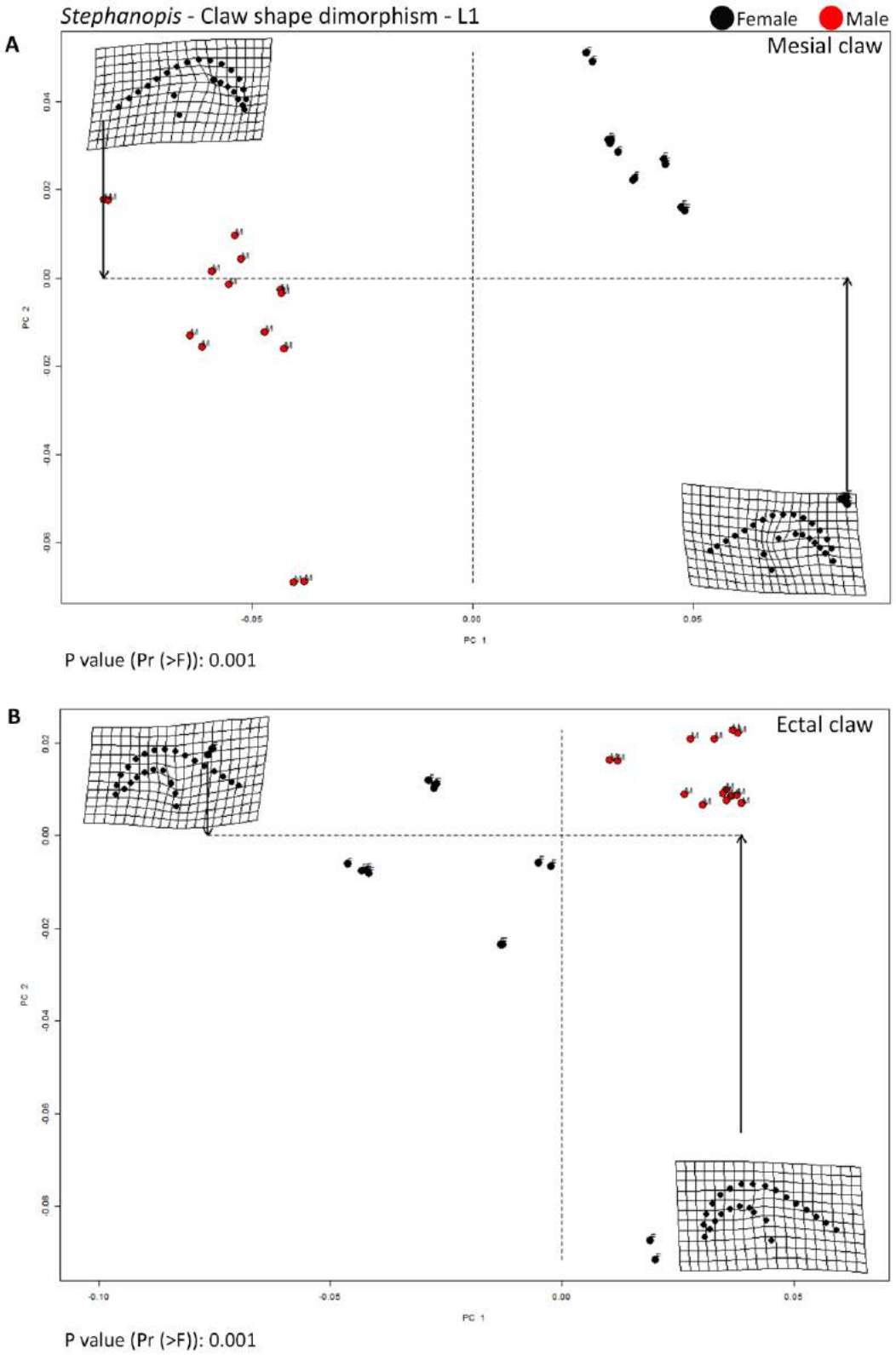
Graphic 21. Principal components analysis showing claws' variation in leg II between males and females of *Sidymella.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



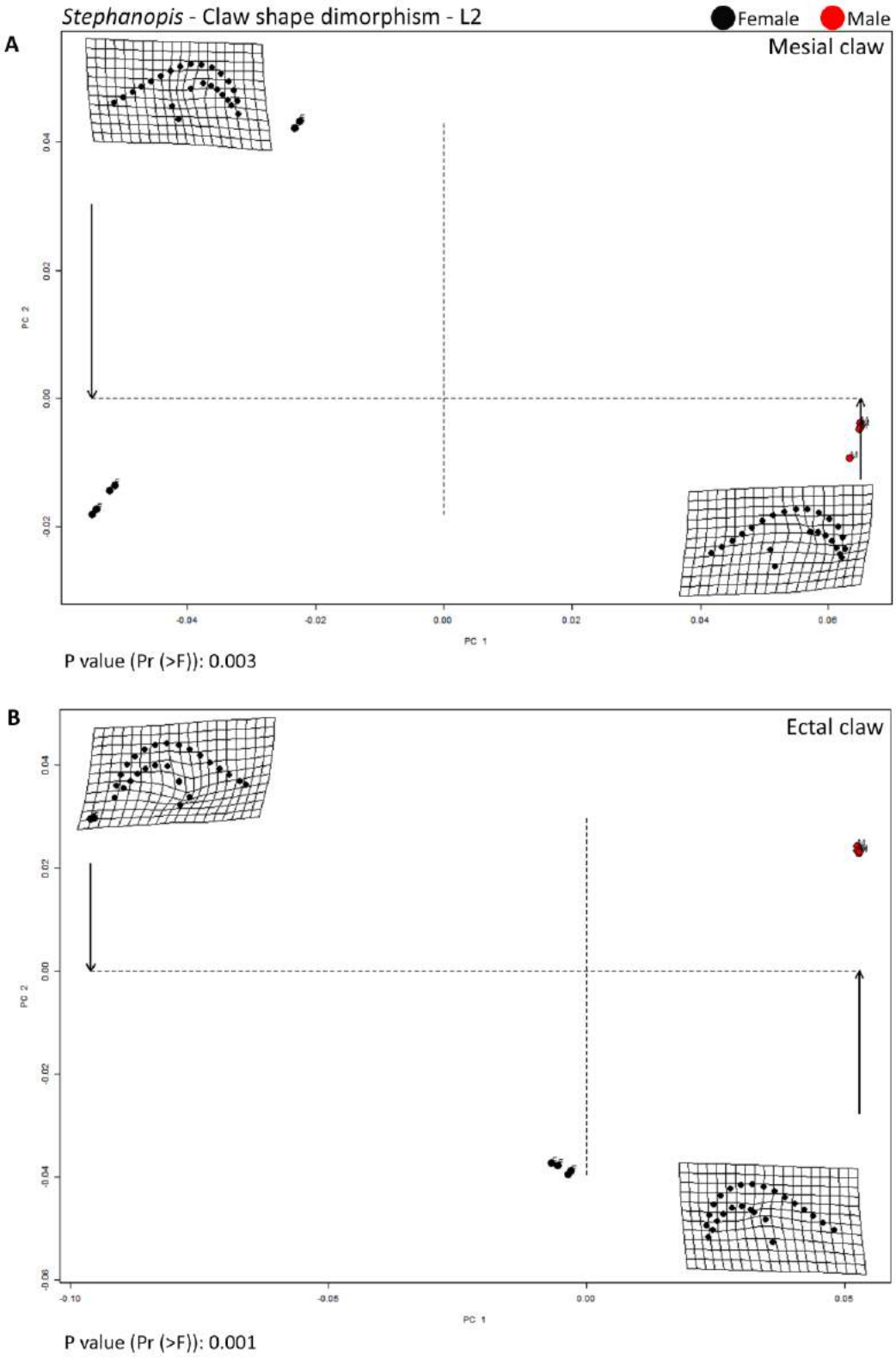
Graphic 22. Principal components analysis showing claws' variation in leg III between males and females of *Sidymella.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



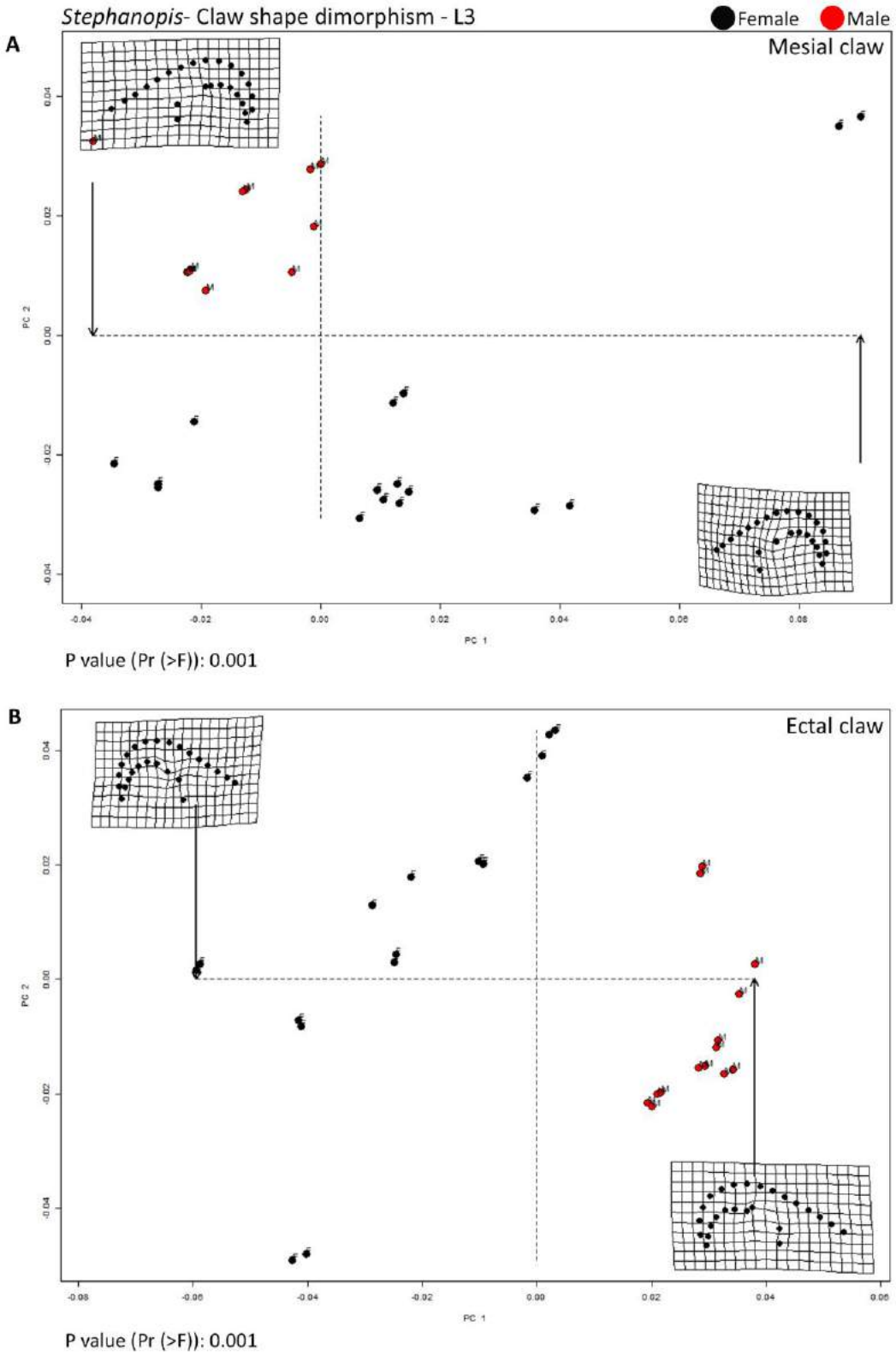
Graphic 23. Principal components analysis showing claws' variation in leg IV between males and females of *Sidymella.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



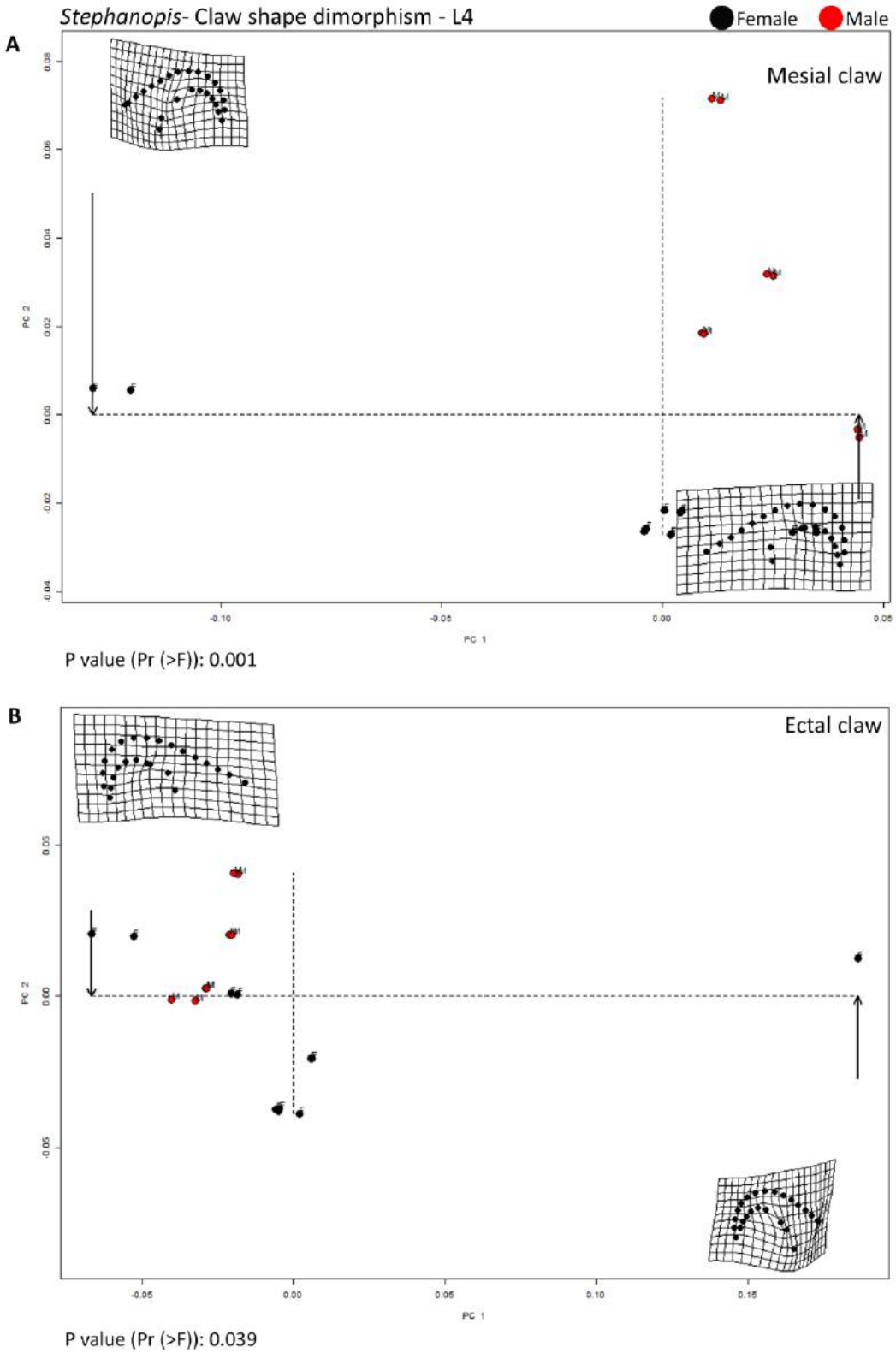
Graphic 24. Principal components analysis showing claws' variation in leg I between males and females of *Stephanopis.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



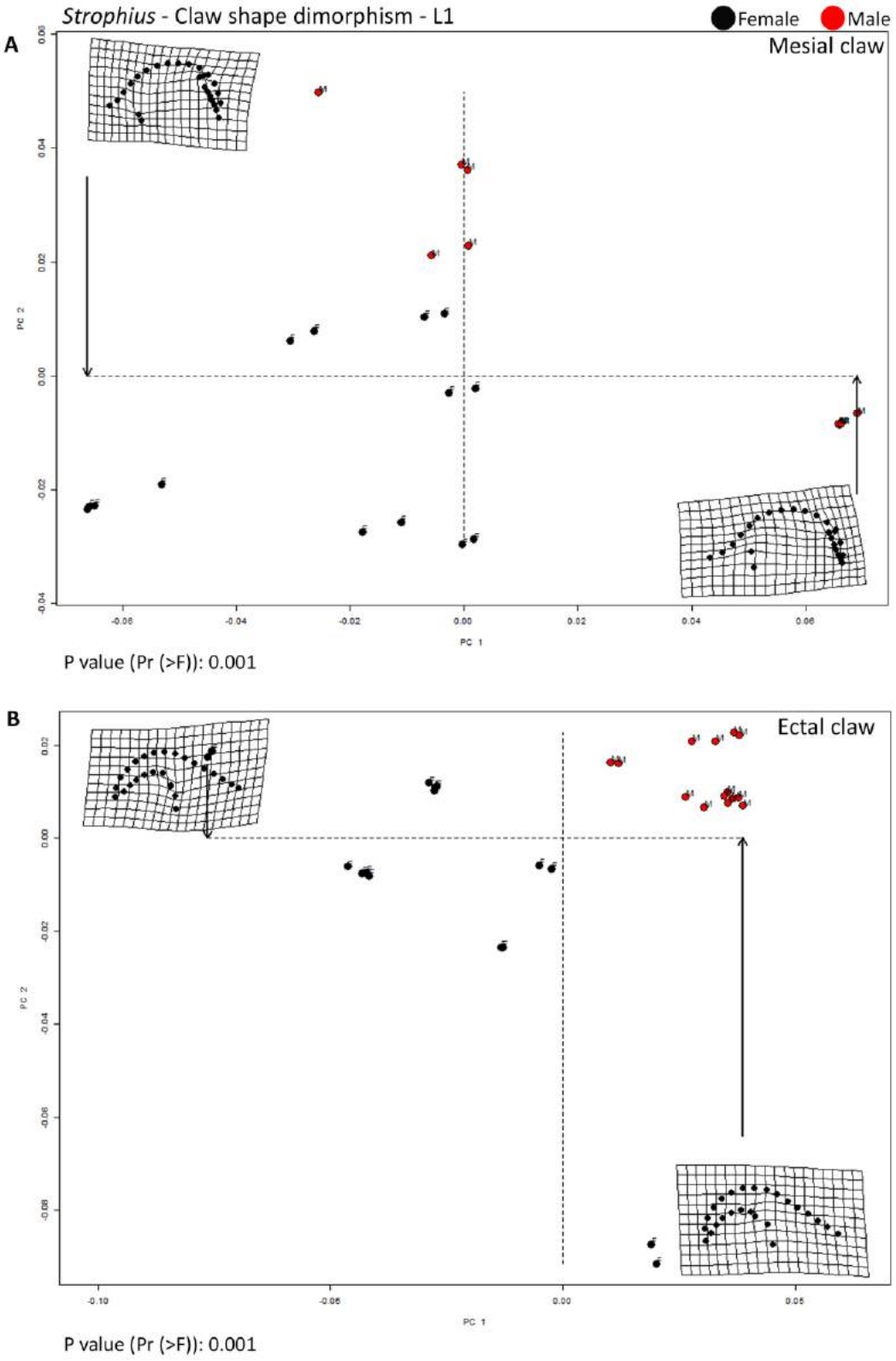
Graphic 25. Principal components analysis showing claws' variation in leg II between males and females of *Stephanopis.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



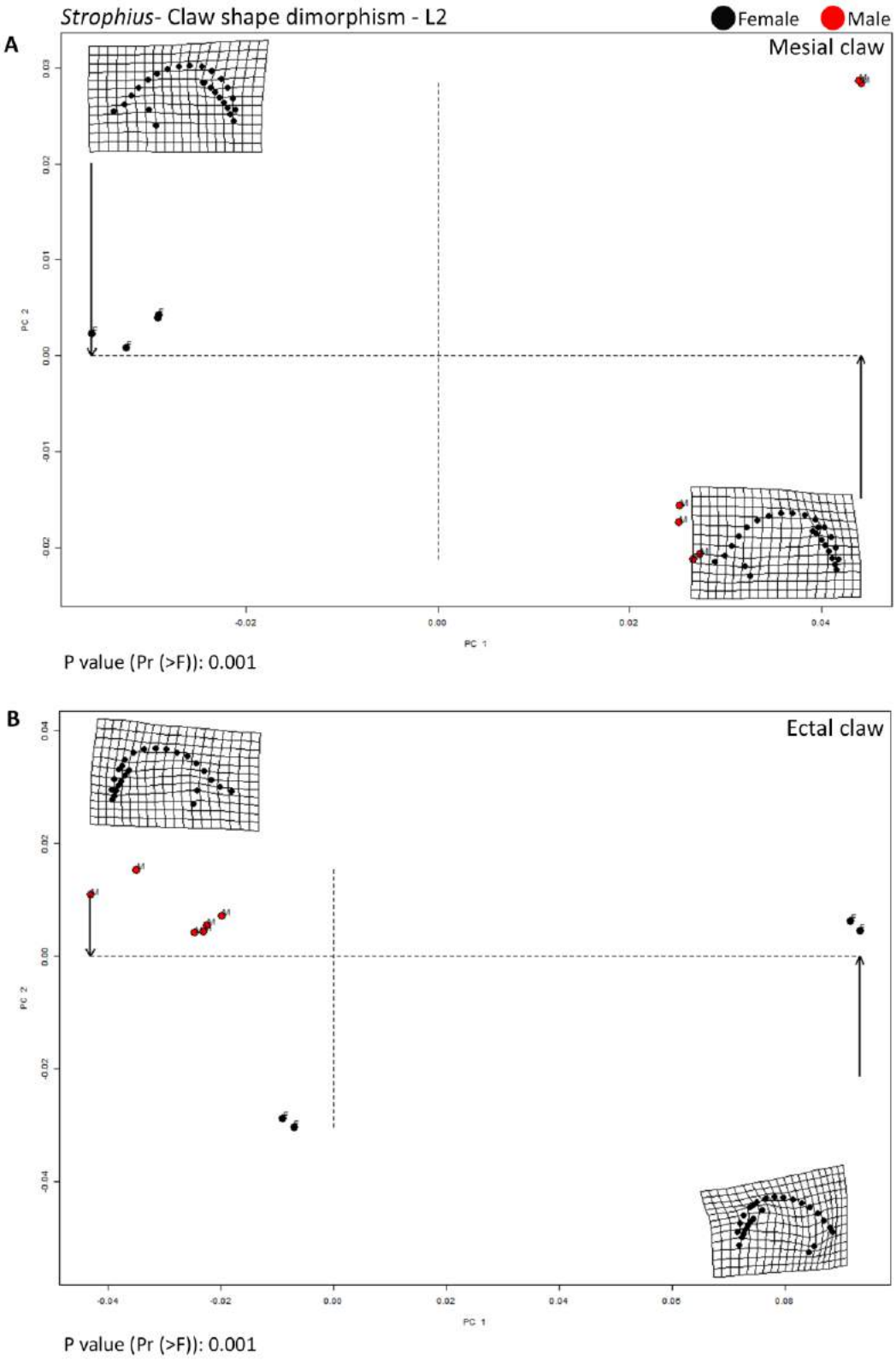
Graphic 26. Principal components analysis showing claws' variation in leg III between males and females of *Stephanopis.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



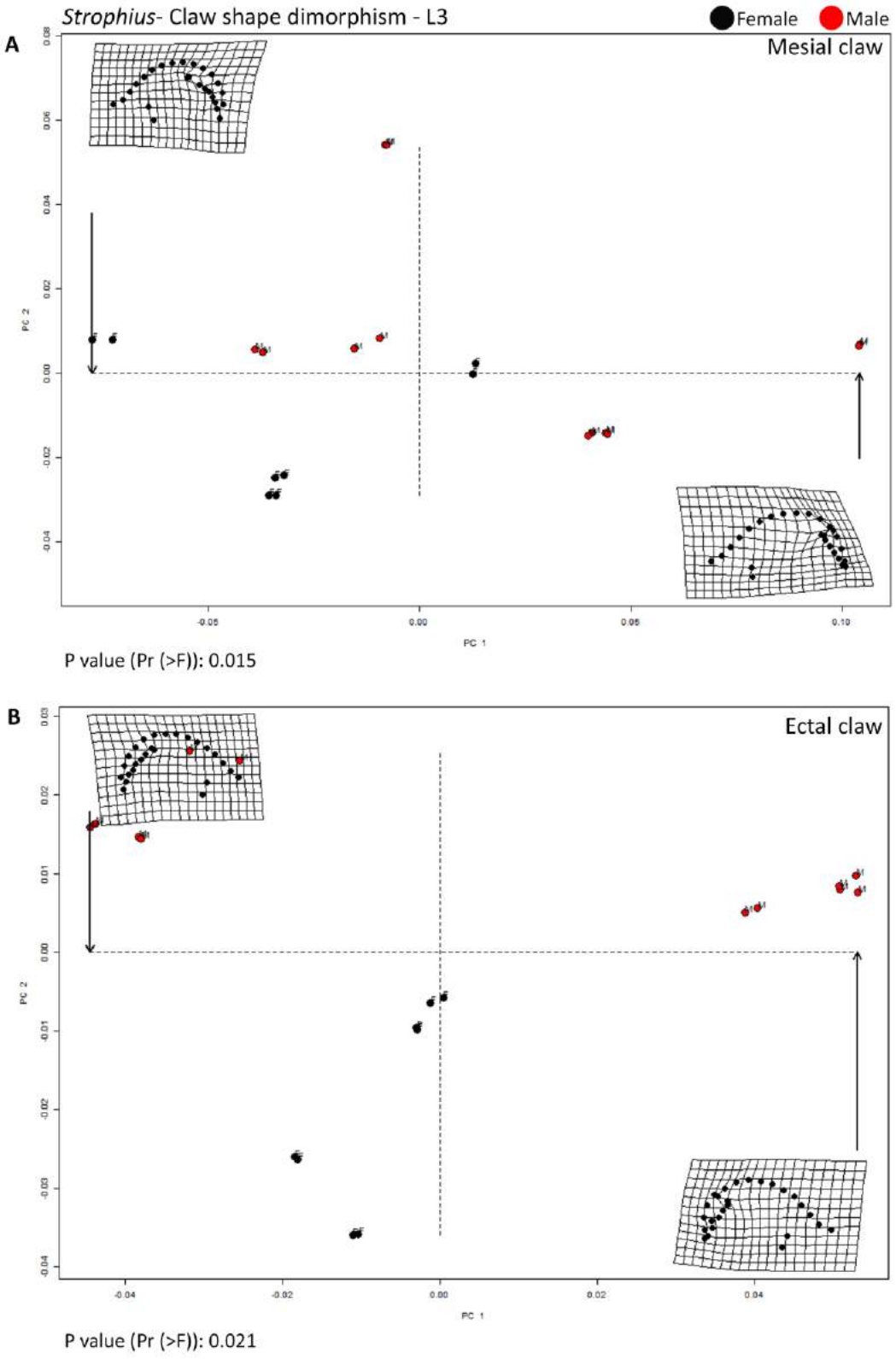
Graphic 27. Principal components analysis showing claws' variation in leg IV between males and females of *Stephanopis.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



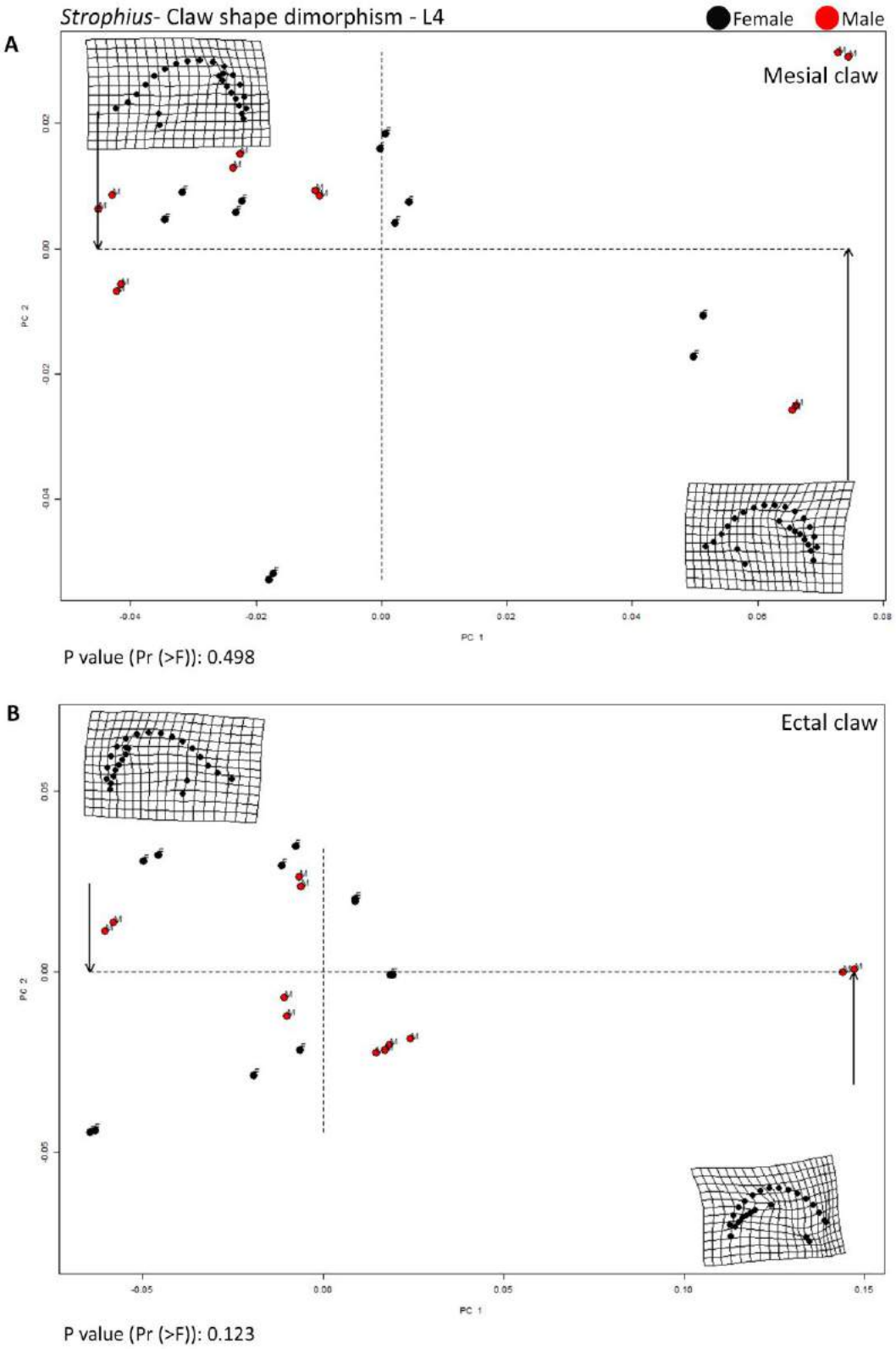
Graphic 28. Principal components analysis showing claws' variation in leg I between males and females of *Strophius.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



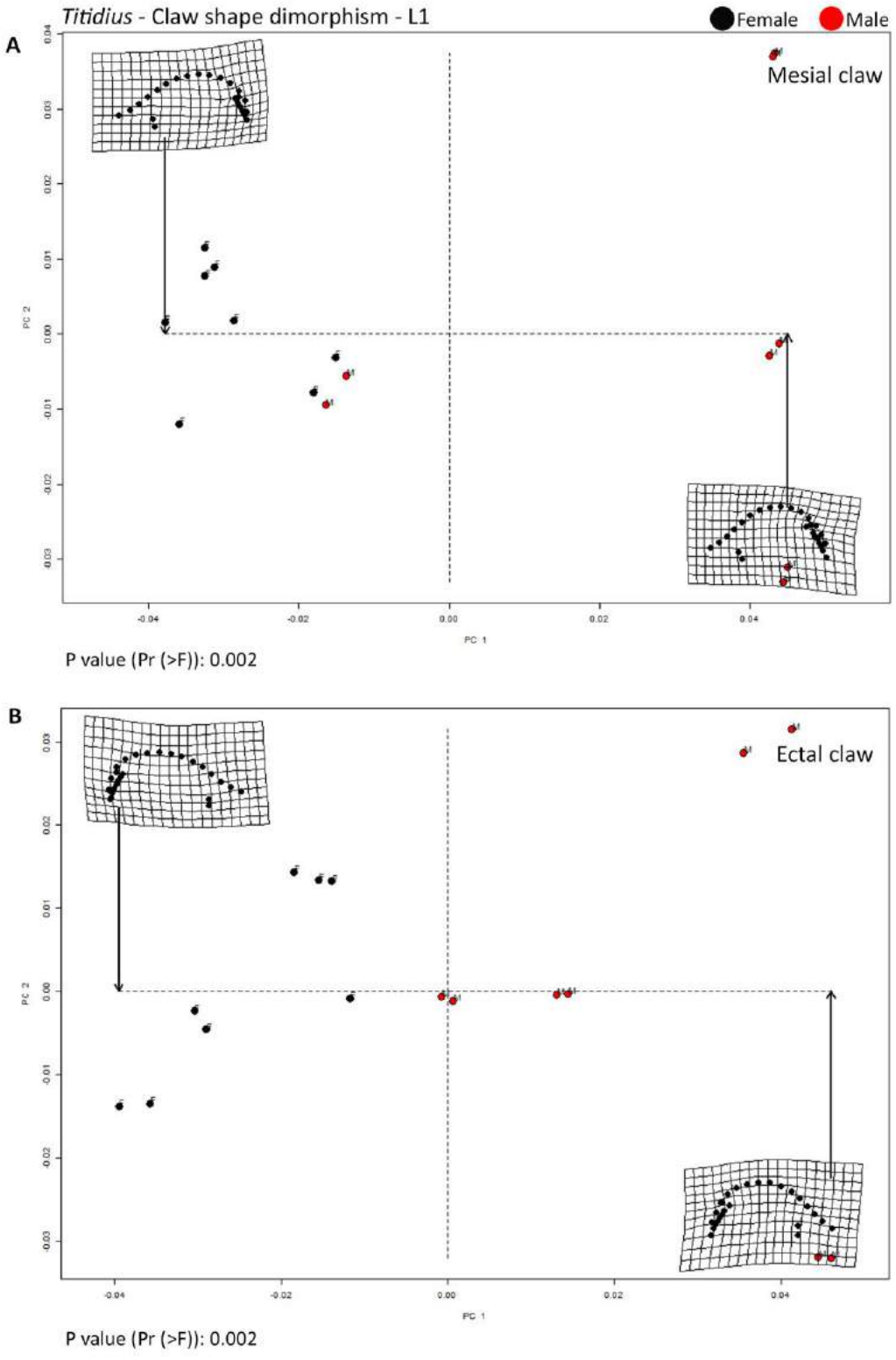
Graphic 29. Principal components analysis showing claws' variation in leg II between males and females of *Strophius*. P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



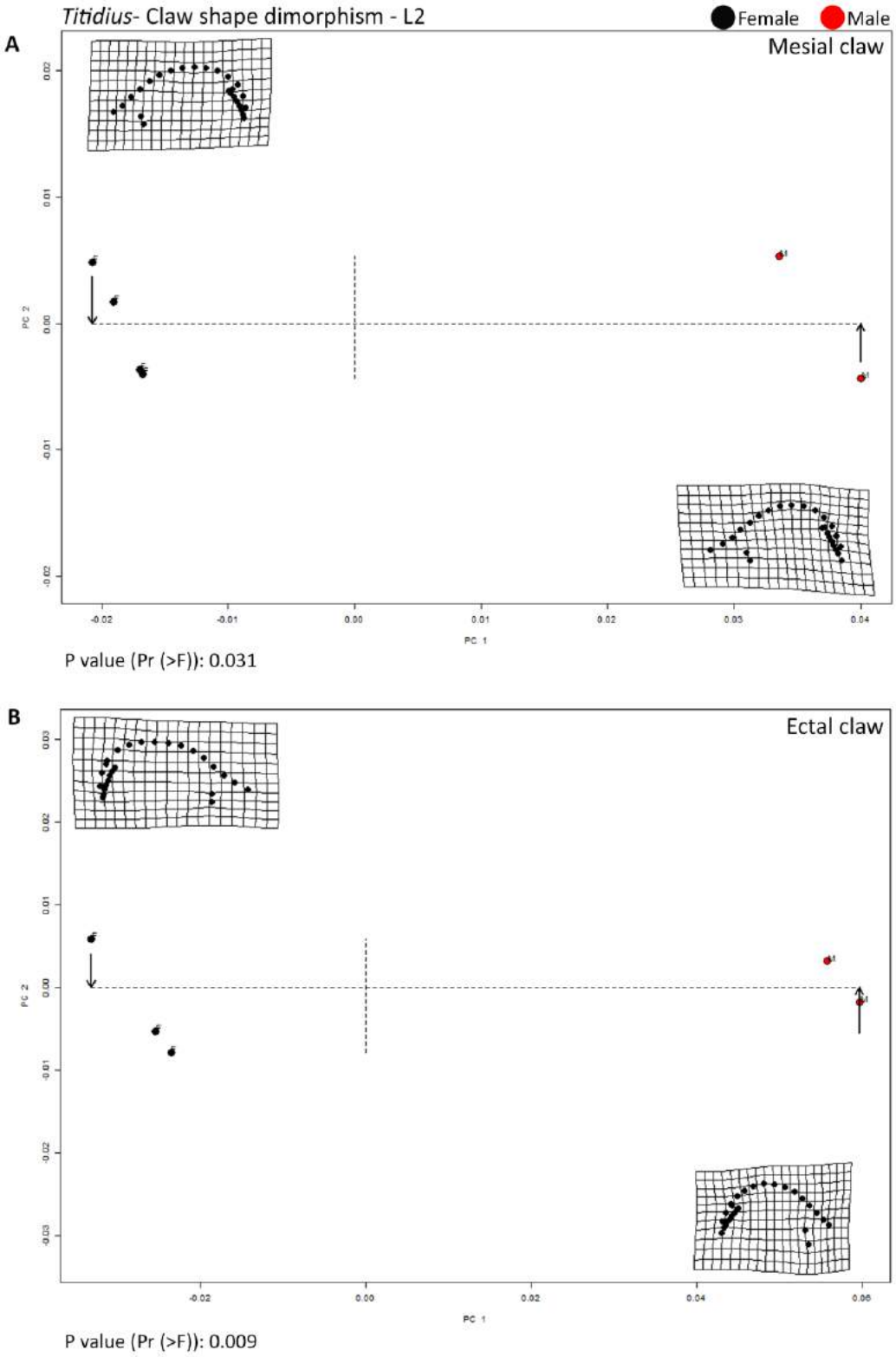
Graphic 30. Principal components analysis showing claws' variation in leg III between males and females of *Strophius.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



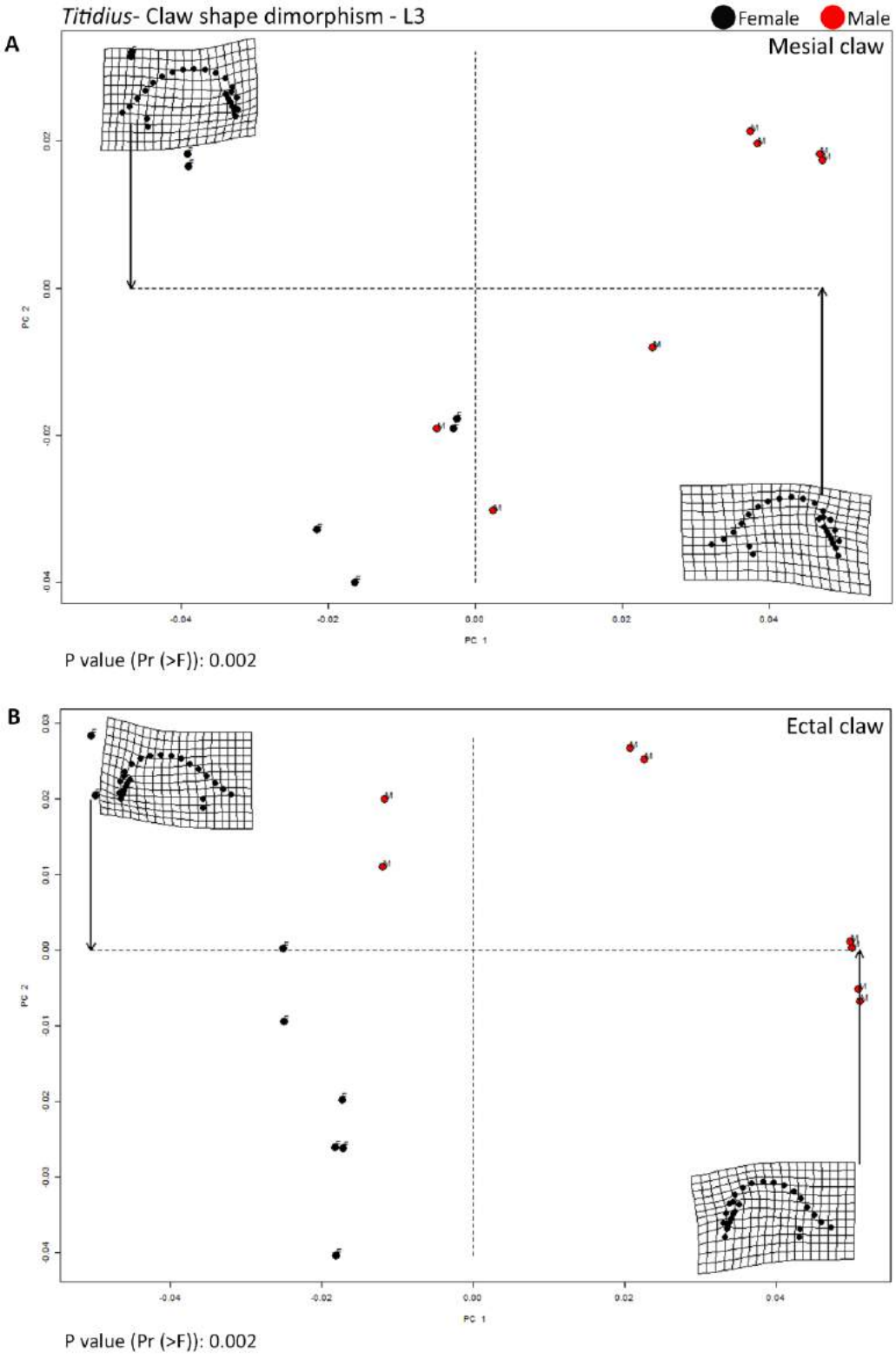
Graphic 31. Principal components analysis showing claws' variation in leg IV between males and females of *Strophius.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



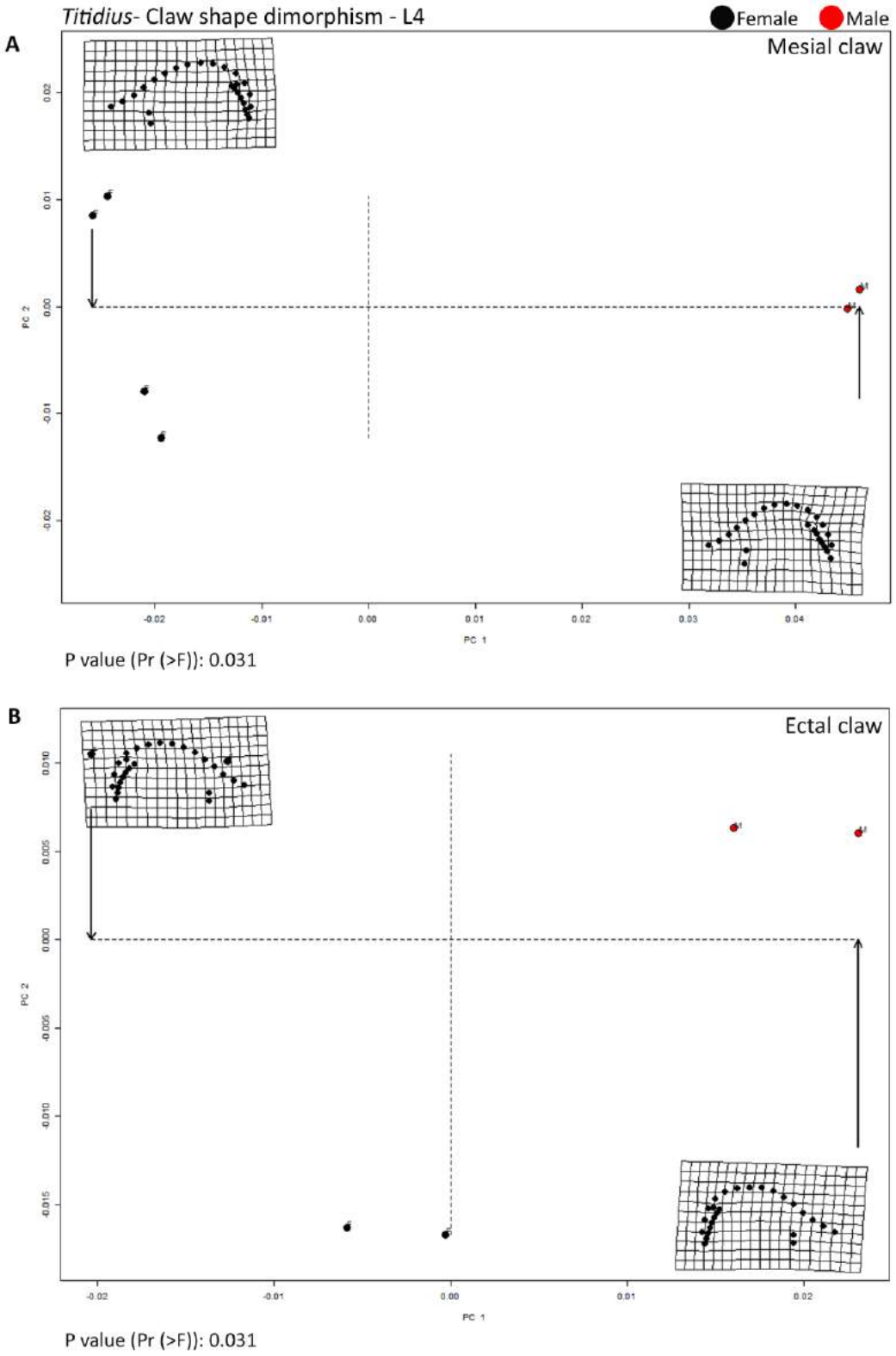
Graphic 32. Principal components analysis showing claws' variation in leg I between males and females of *Titidius* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



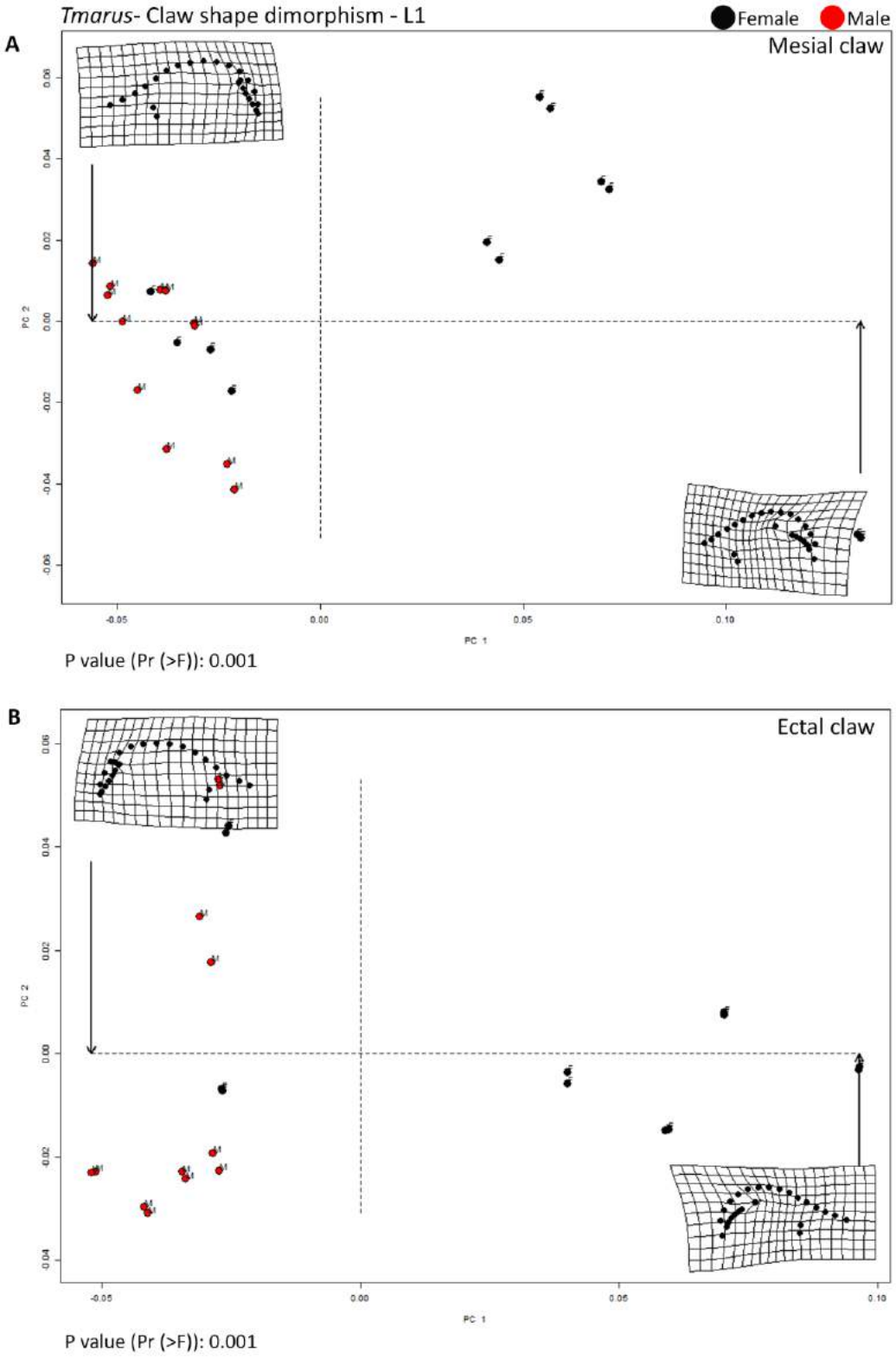
Graphic 33. Principal components analysis showing claws' variation in leg II between males and females of *Titidius.* P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



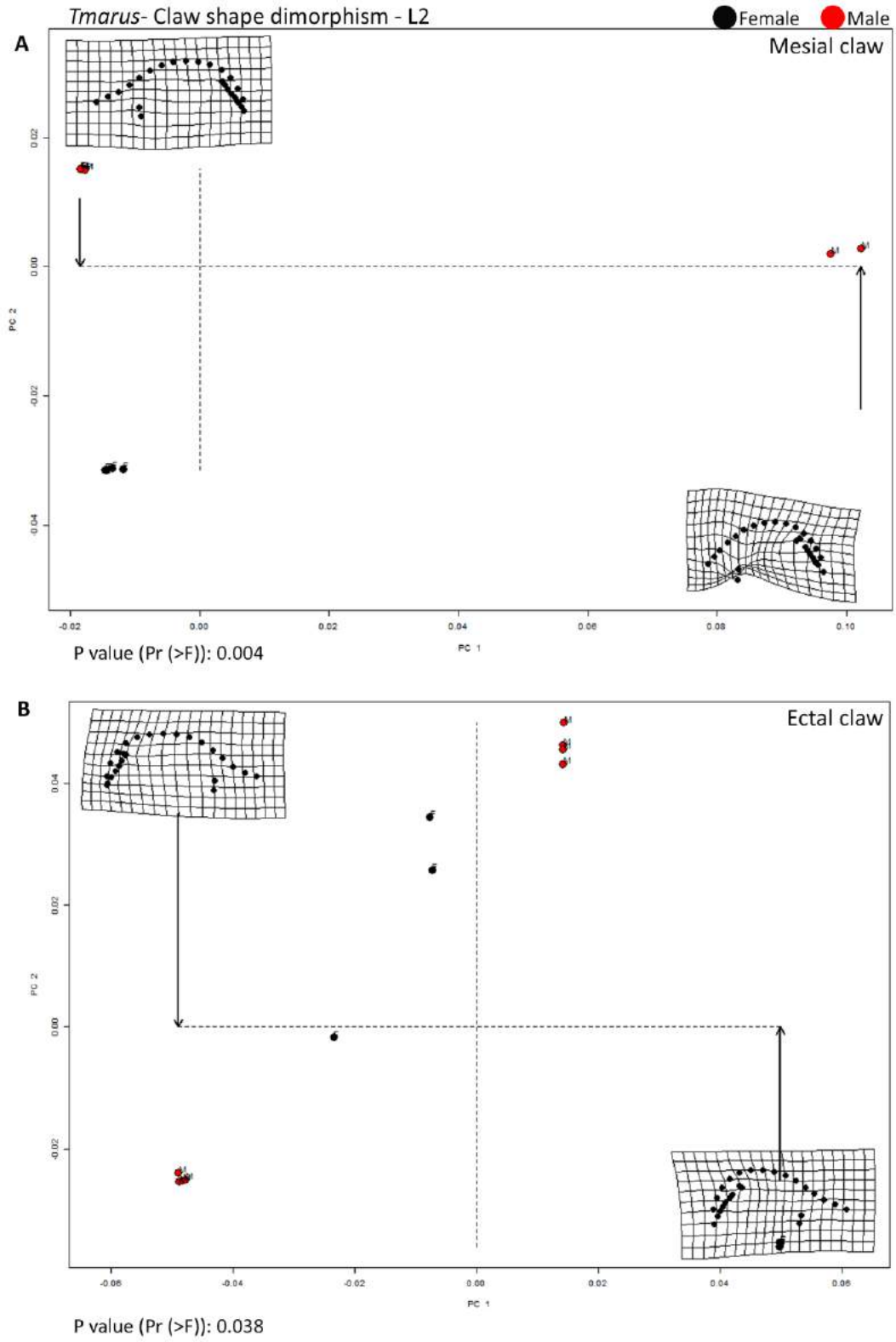
Graphic 34. Principal components analysis showing claws' variation in leg III between males and females of *Titidius*. P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



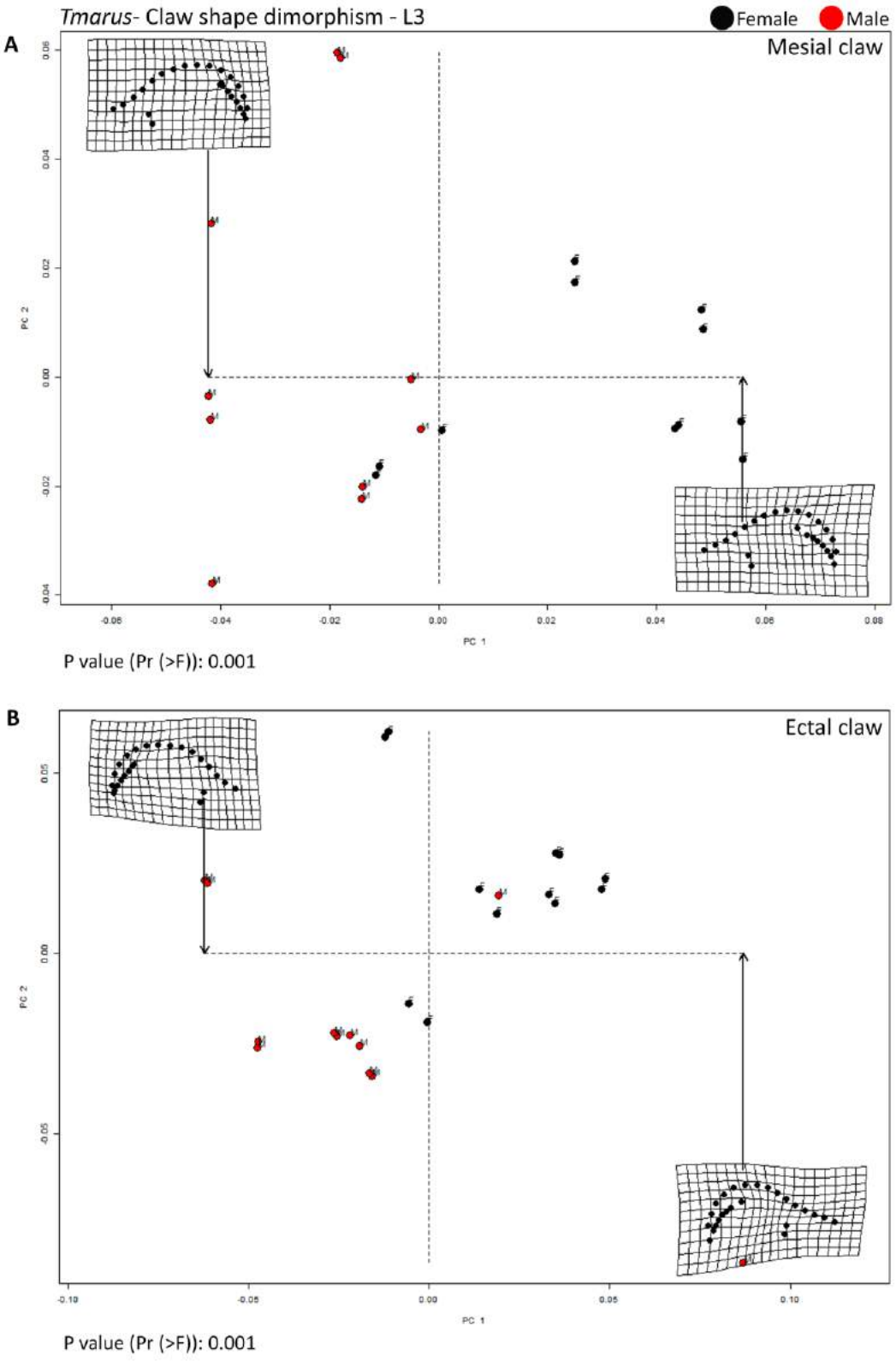
Graphic 35. Principal components analysis showing claws' variation in leg IV between males and females of *Titidius*. P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



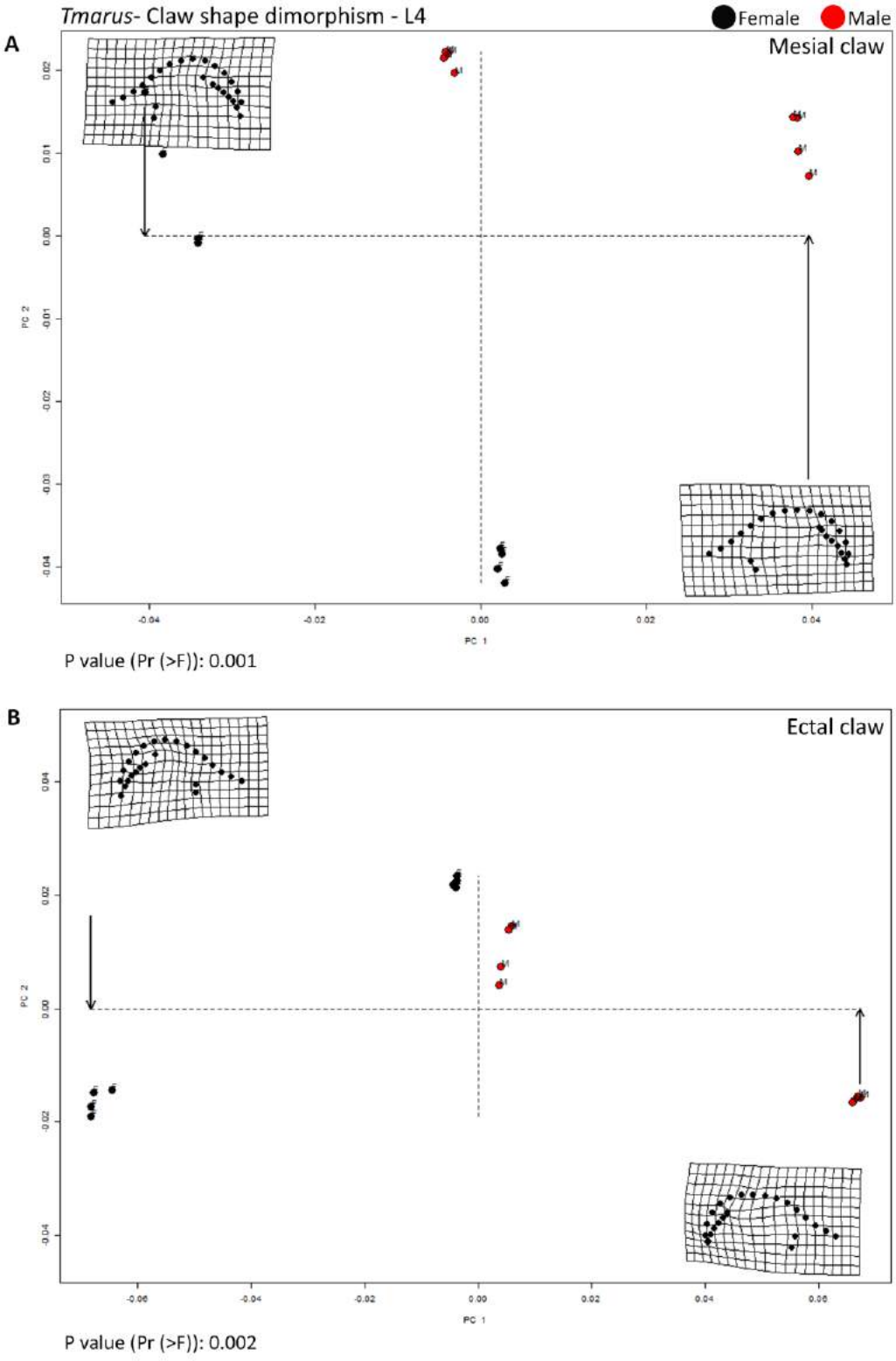
Graphic 36. Principal components analysis showing claws' variation in leg I between males and females of *Tmarus*. P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



Graphic 37. Principal components analysis showing claws' variation in leg I between males and females of *Tmarus*. P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



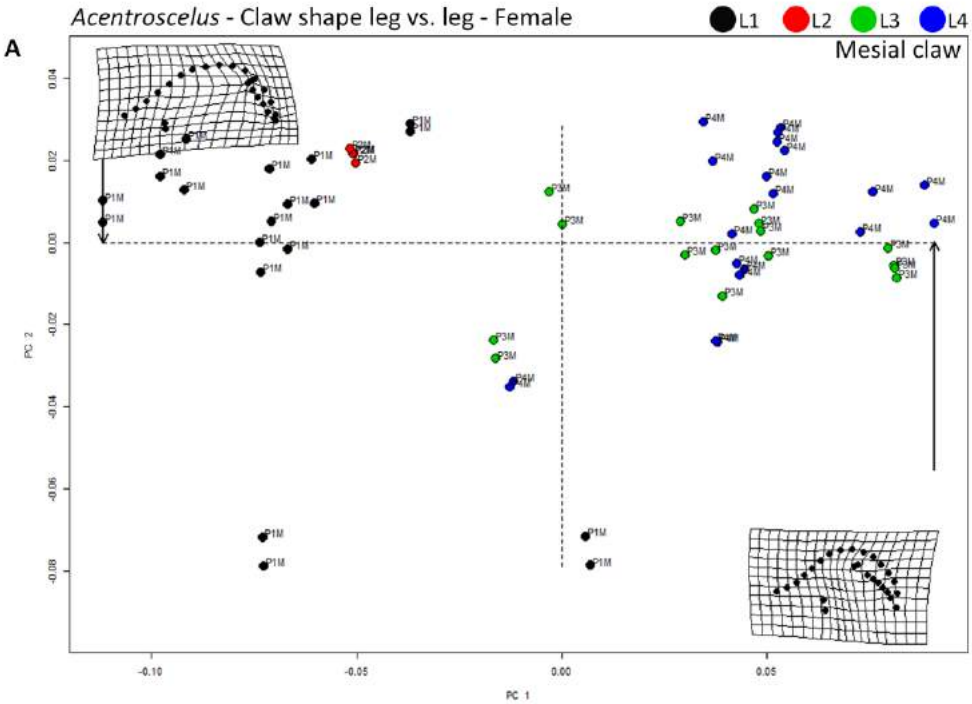
Graphic 38. Principal components analysis showing claws' variation in leg I between males and females of *Tmarus*. P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively

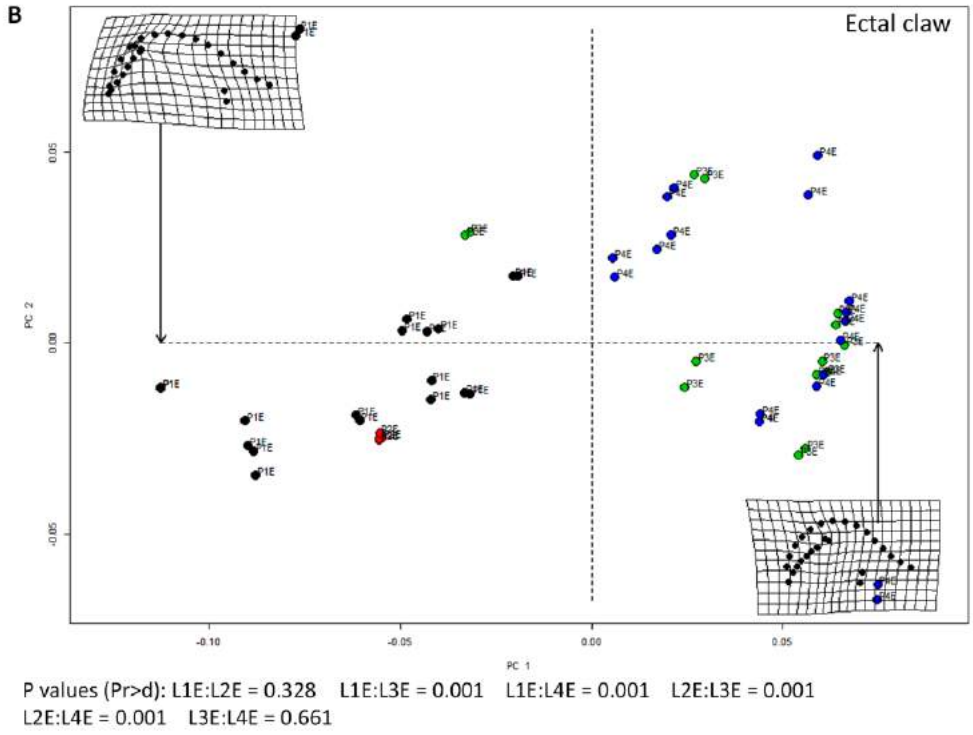


Graphic 39. Principal components analysis showing claws' variation in leg I between males and females of *Tmarus*. P-value of MANOVA comparison are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively

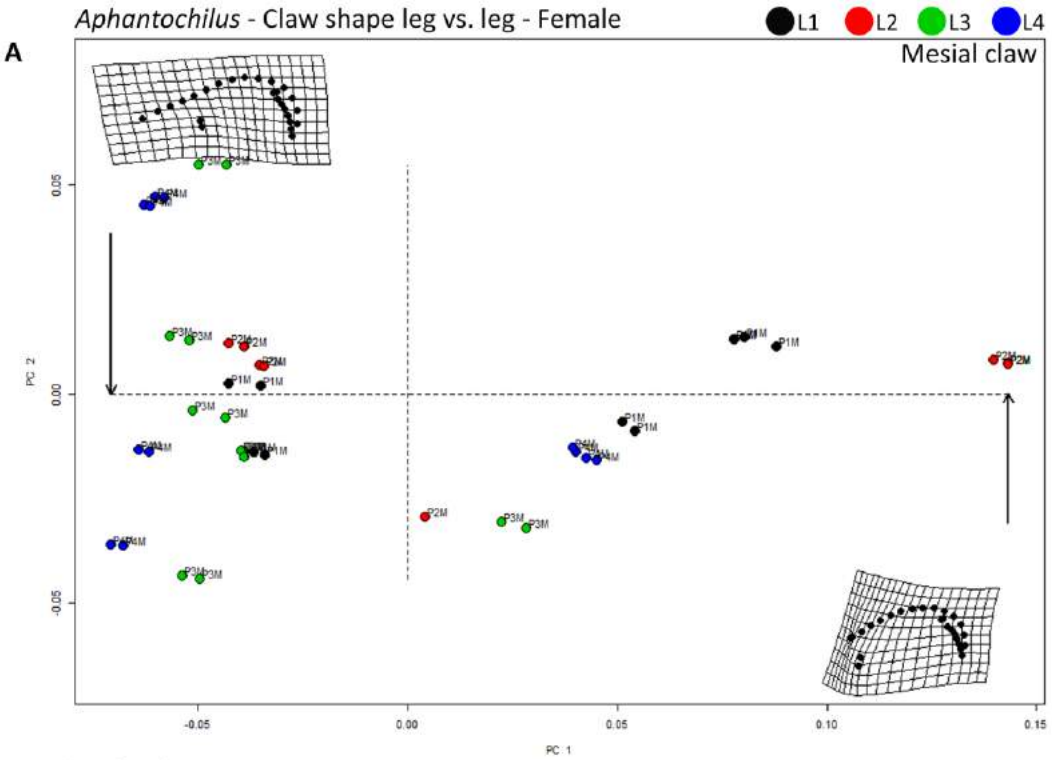
APPENDIX 5

Principal Component Analyses and p-values of MANOVA pairwise comparisons between homologous claws in different legs, treating males and females separately.

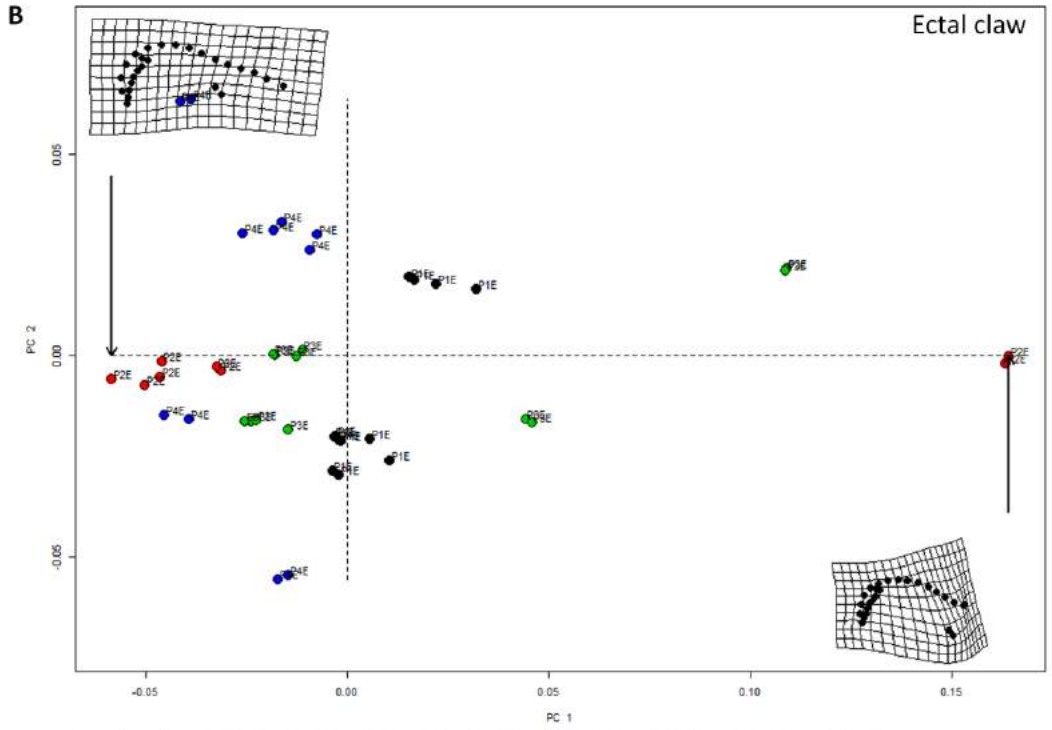




Graphic 1. Principal components analysis showing variation in homologous claws between legs in females of *Acentroscelus*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively

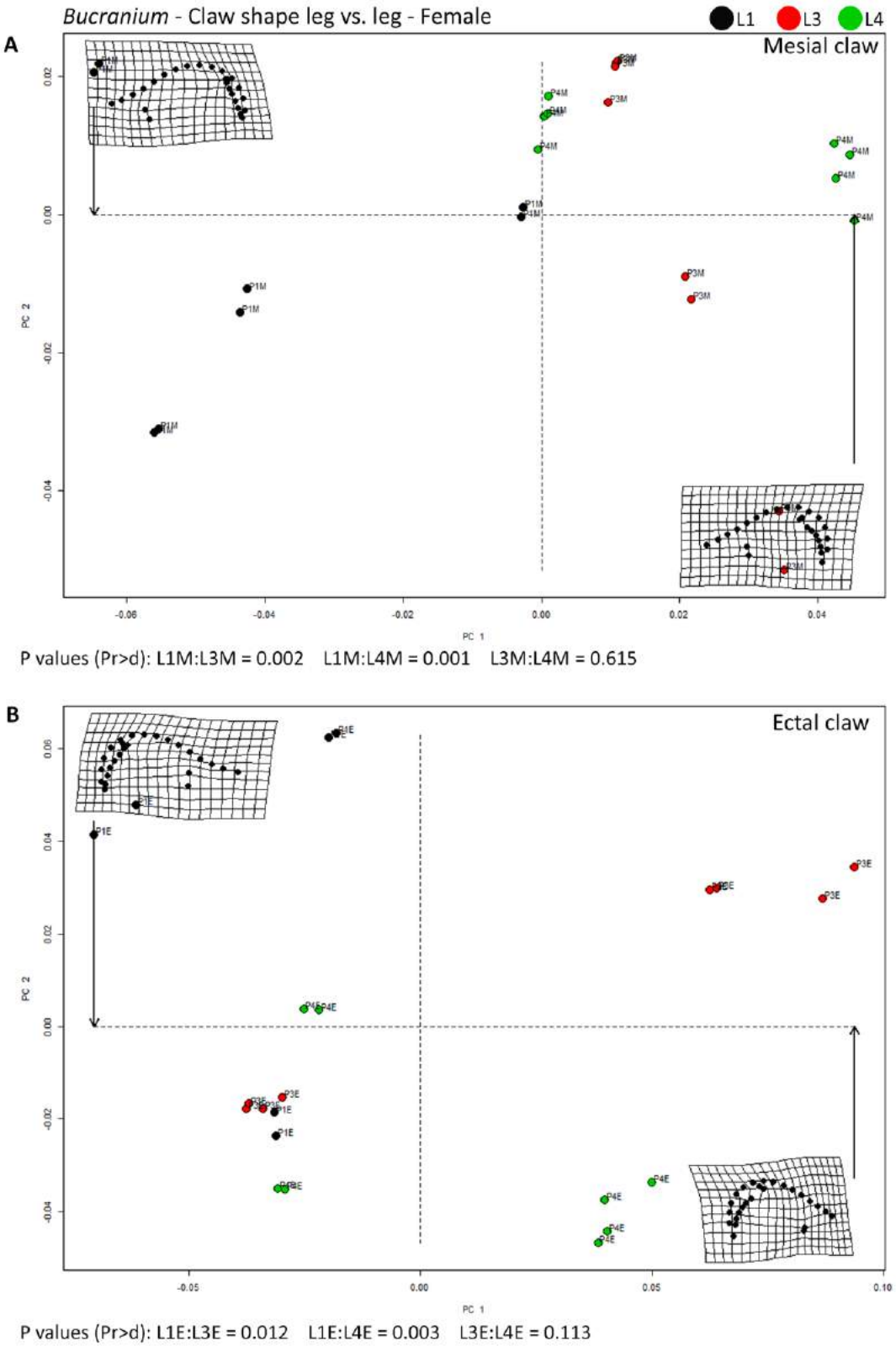


P values (Pr>d): L1M:L2M = 0.1 L1M:L3M = 0.073 L1M:L4M = 0.084 L2M:L3M = 0.003
L2M:L4M = 0.006 L3M:L4M = 0.809

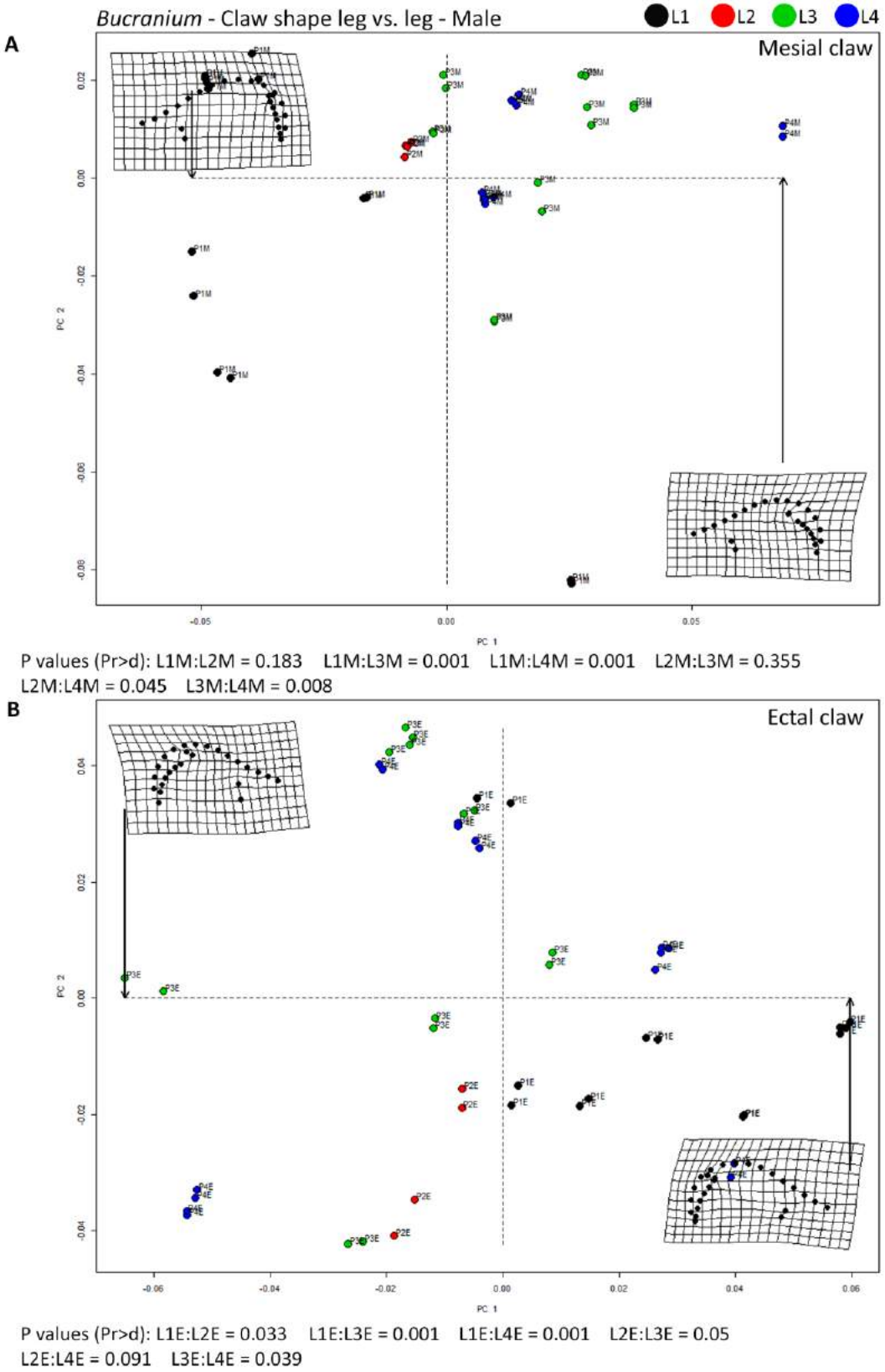


P values (Pr>d): L1E:L2E = 0.595 L1E:L3E = 0.696 L1E:L4E = 0.038 L2E:L3E = 0.416
L2E:L4E = 0.067 L3E:L4E = 0.045

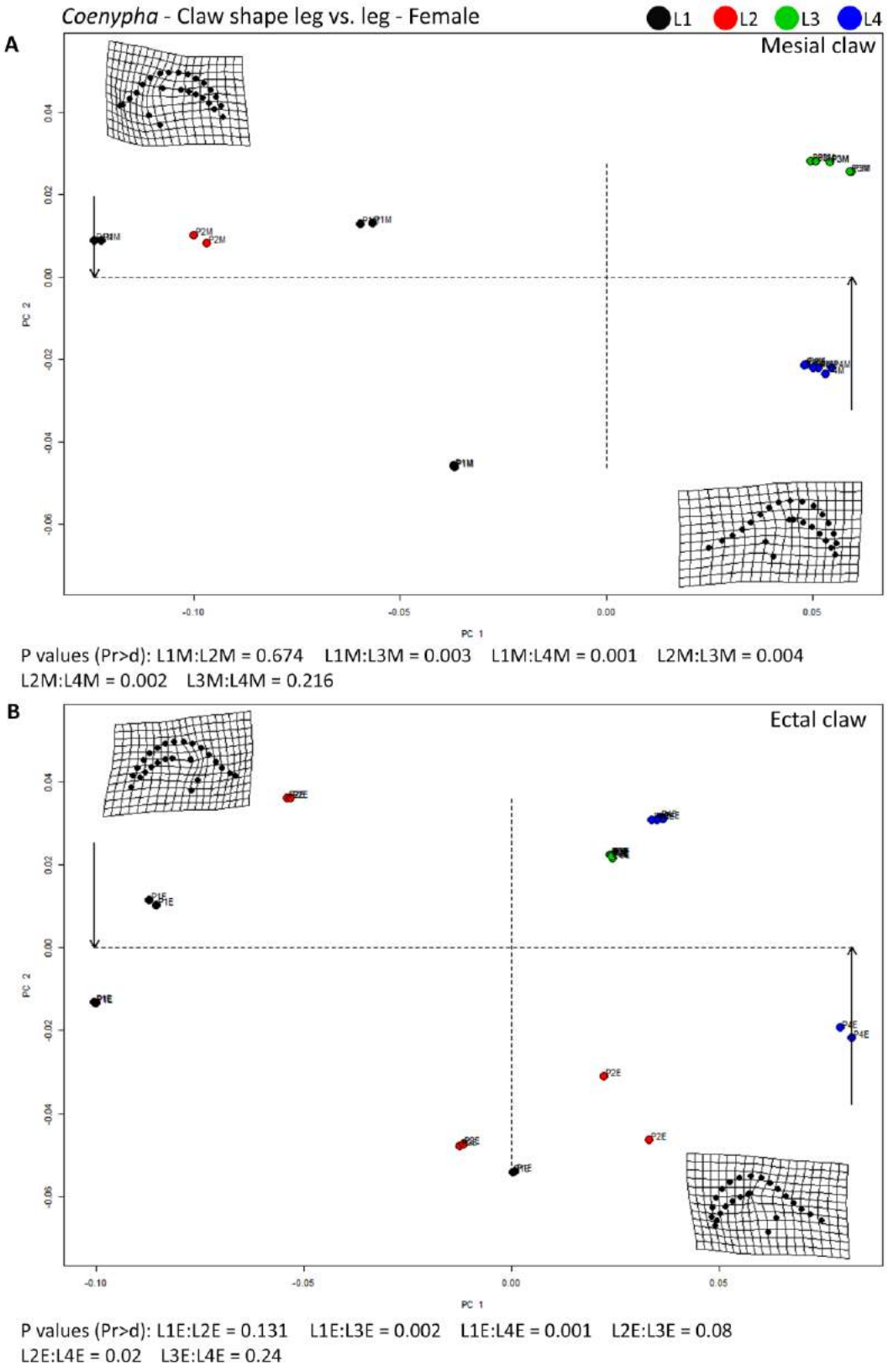
Graphic 2. Principal components analysis showing variation in homologous claws between legs in females of *Aphantochilus*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



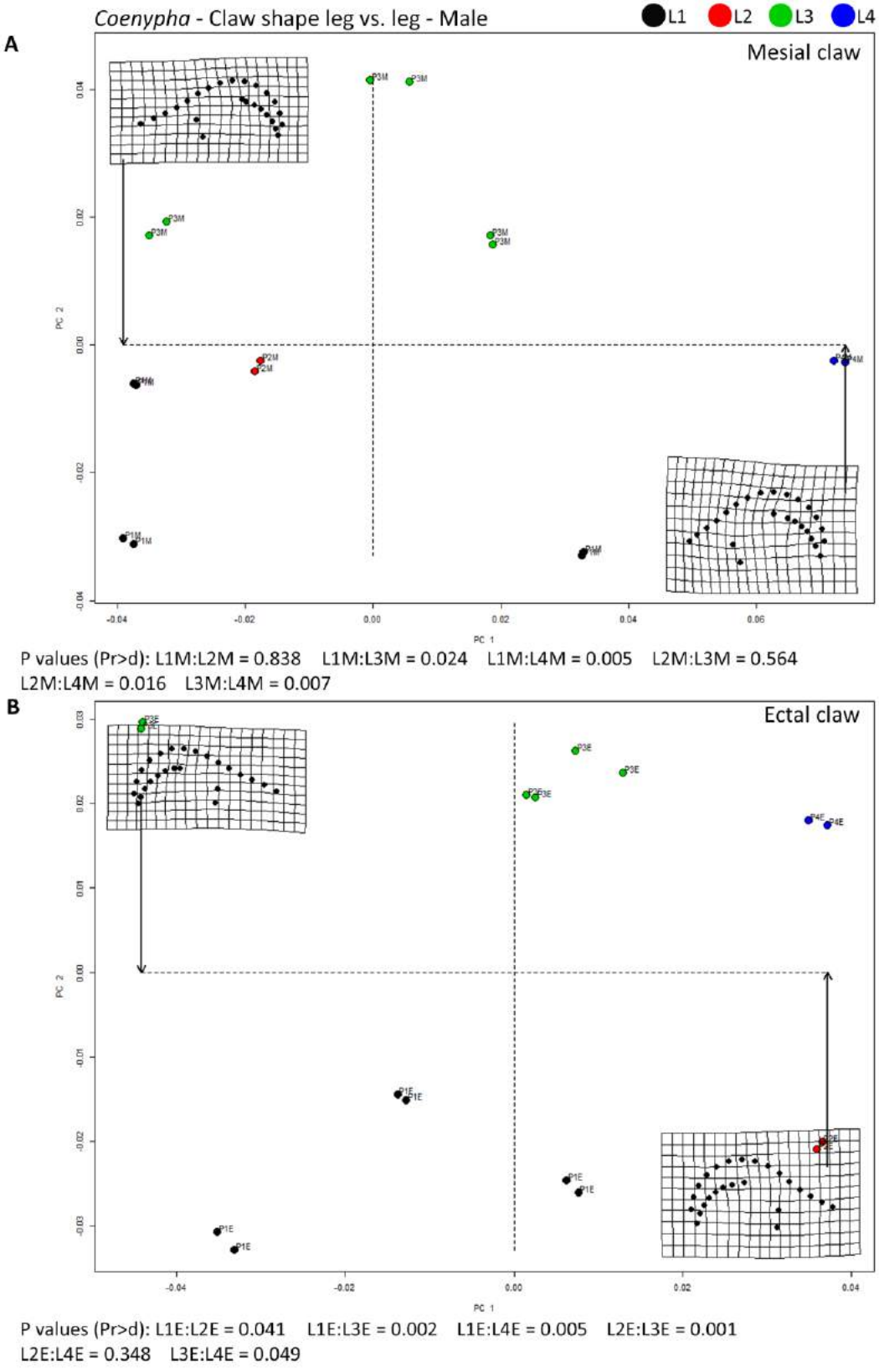
Graphic 3. Principal components analysis showing variation in homologous claws between legs in females of *Bucranium*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



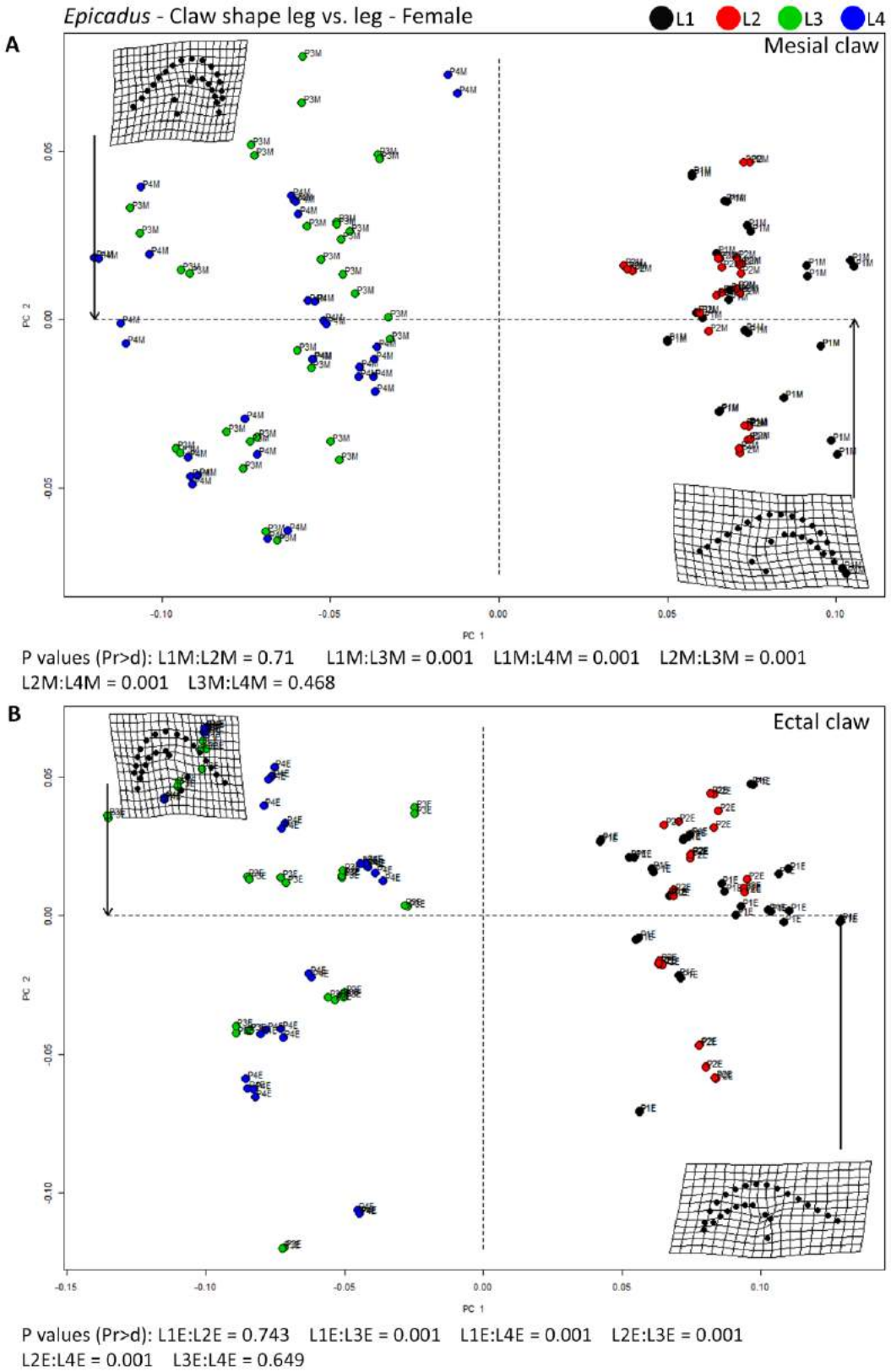
Graphic 4. Principal components analysis showing variation in homologous claws between legs in males of *Bucranium*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



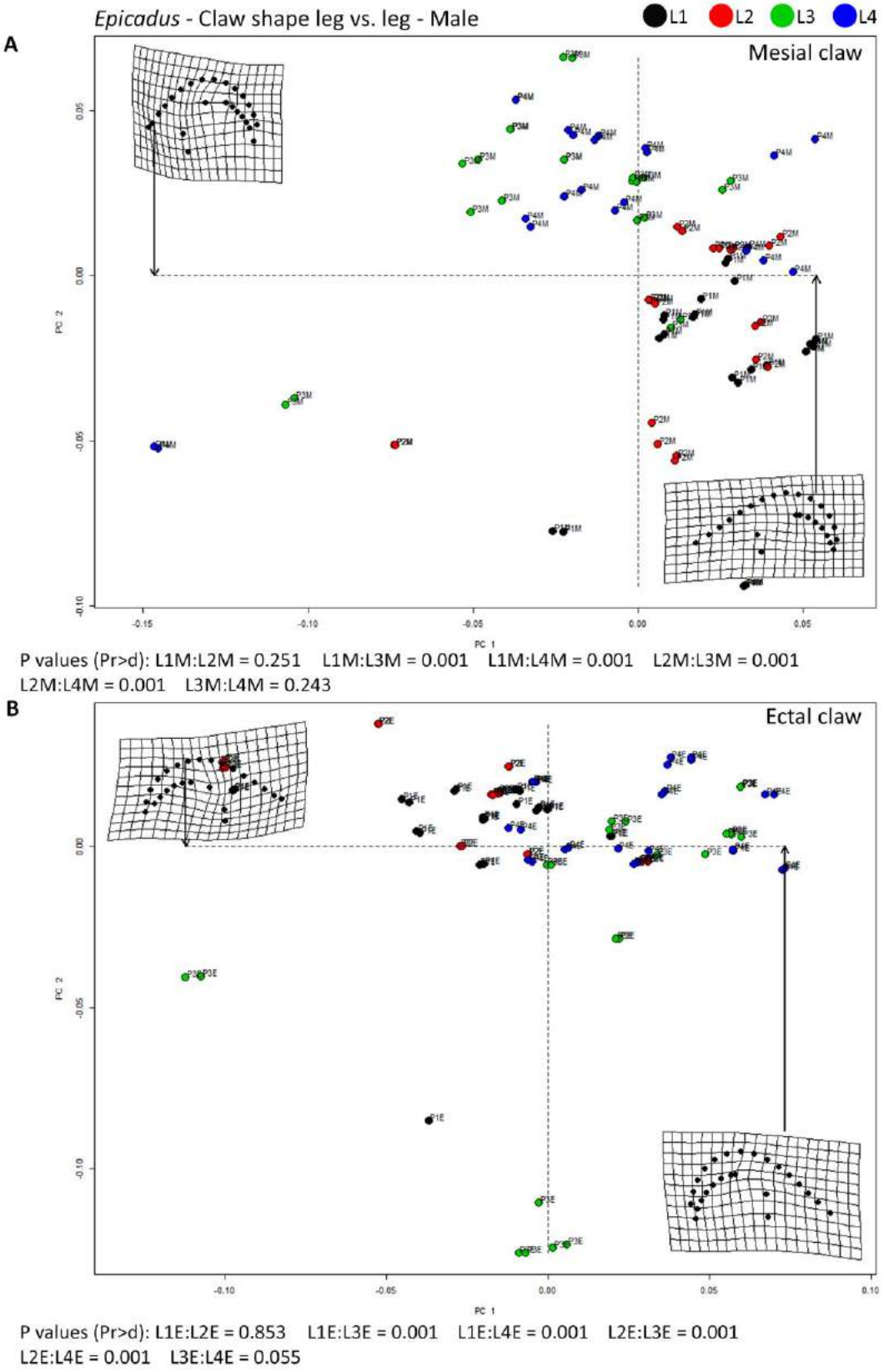
Graphic 5. Principal components analysis showing variation in homologous claws between legs in females of *Coenypha*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



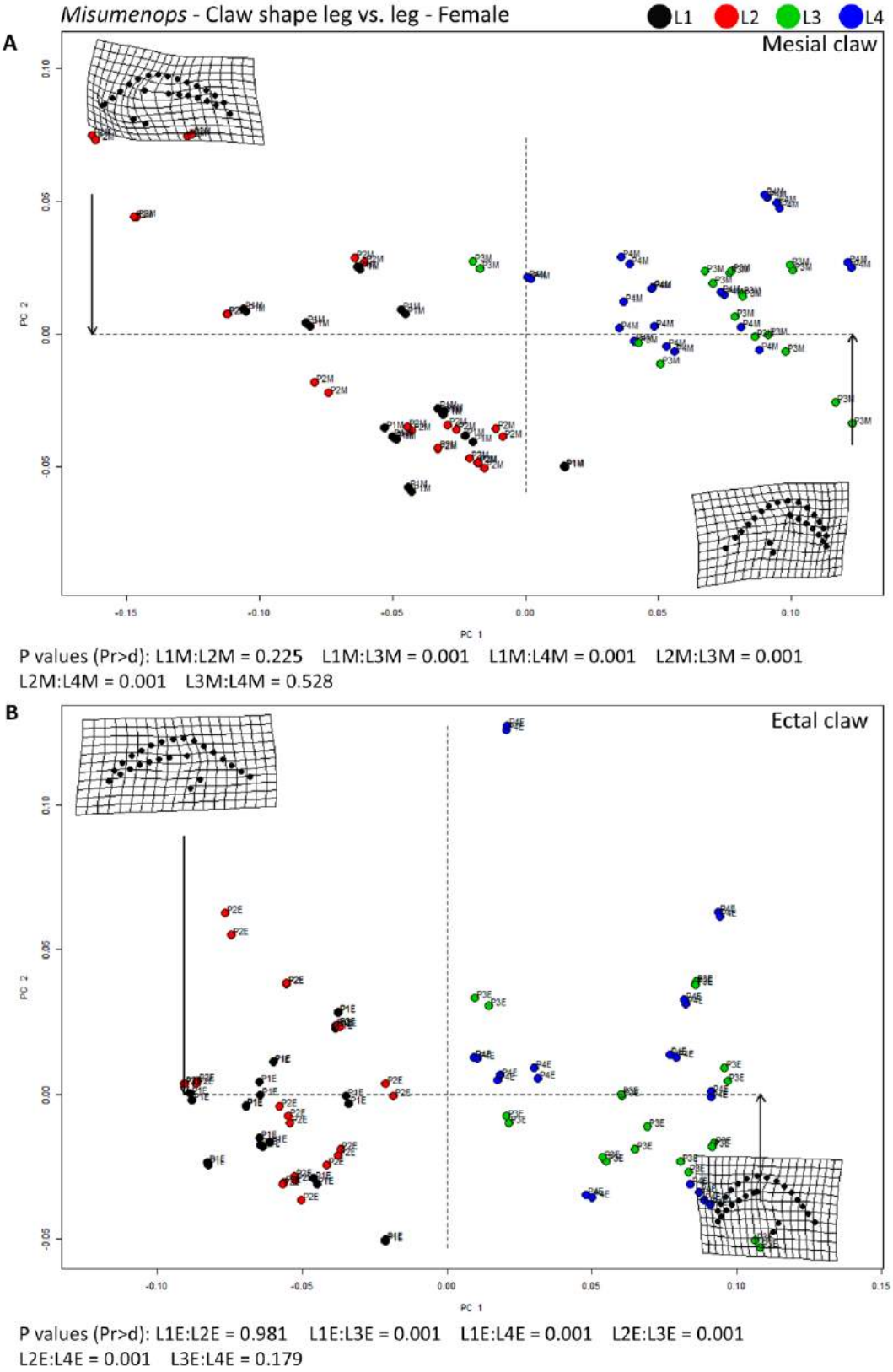
Graphic 6. Principal components analysis showing variation in homologous claws between legs in males of *Coenypha*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



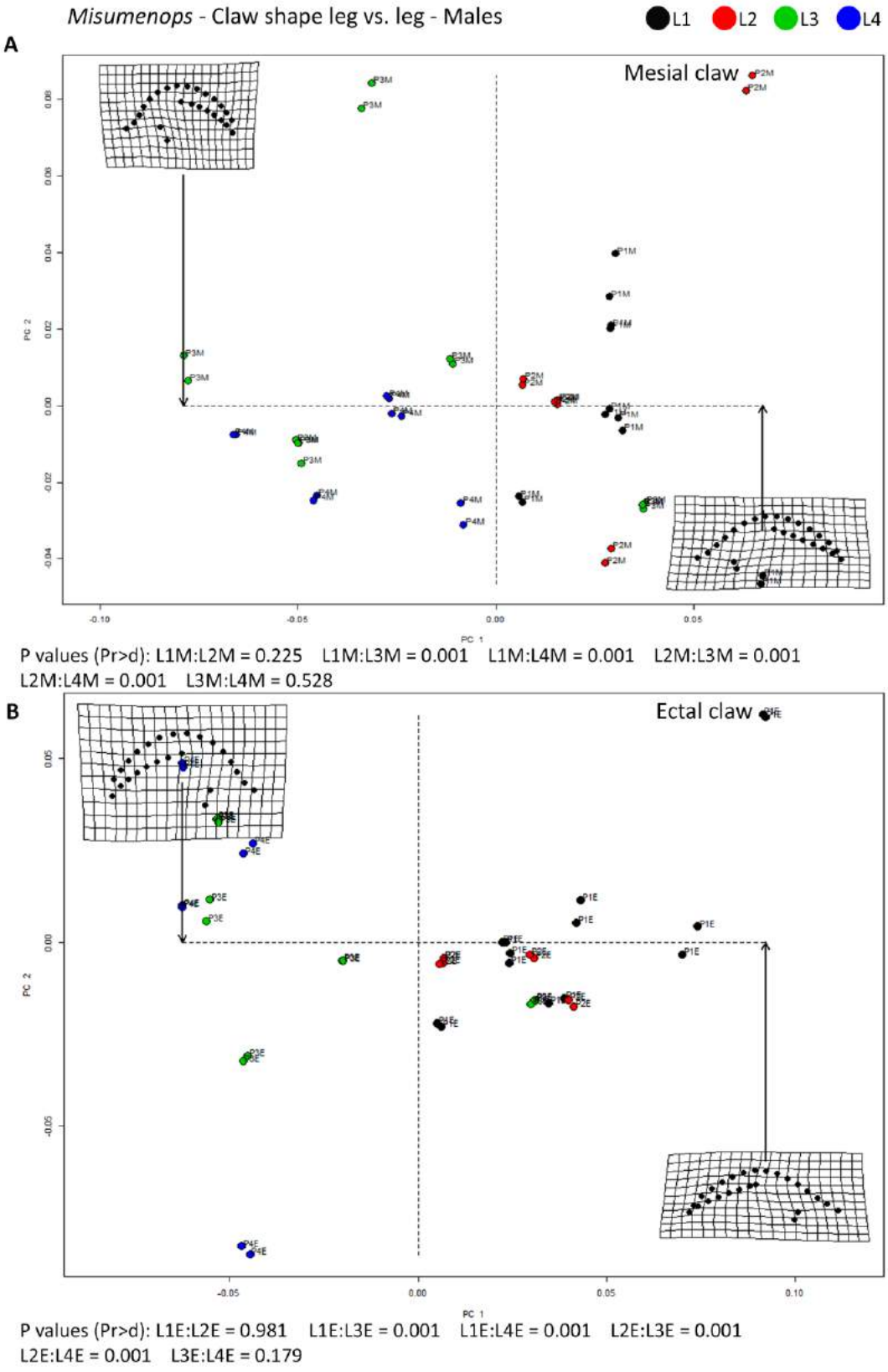
Graphic 7. Principal components analysis showing variation in homologous claws between legs in females of *Epicadus.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



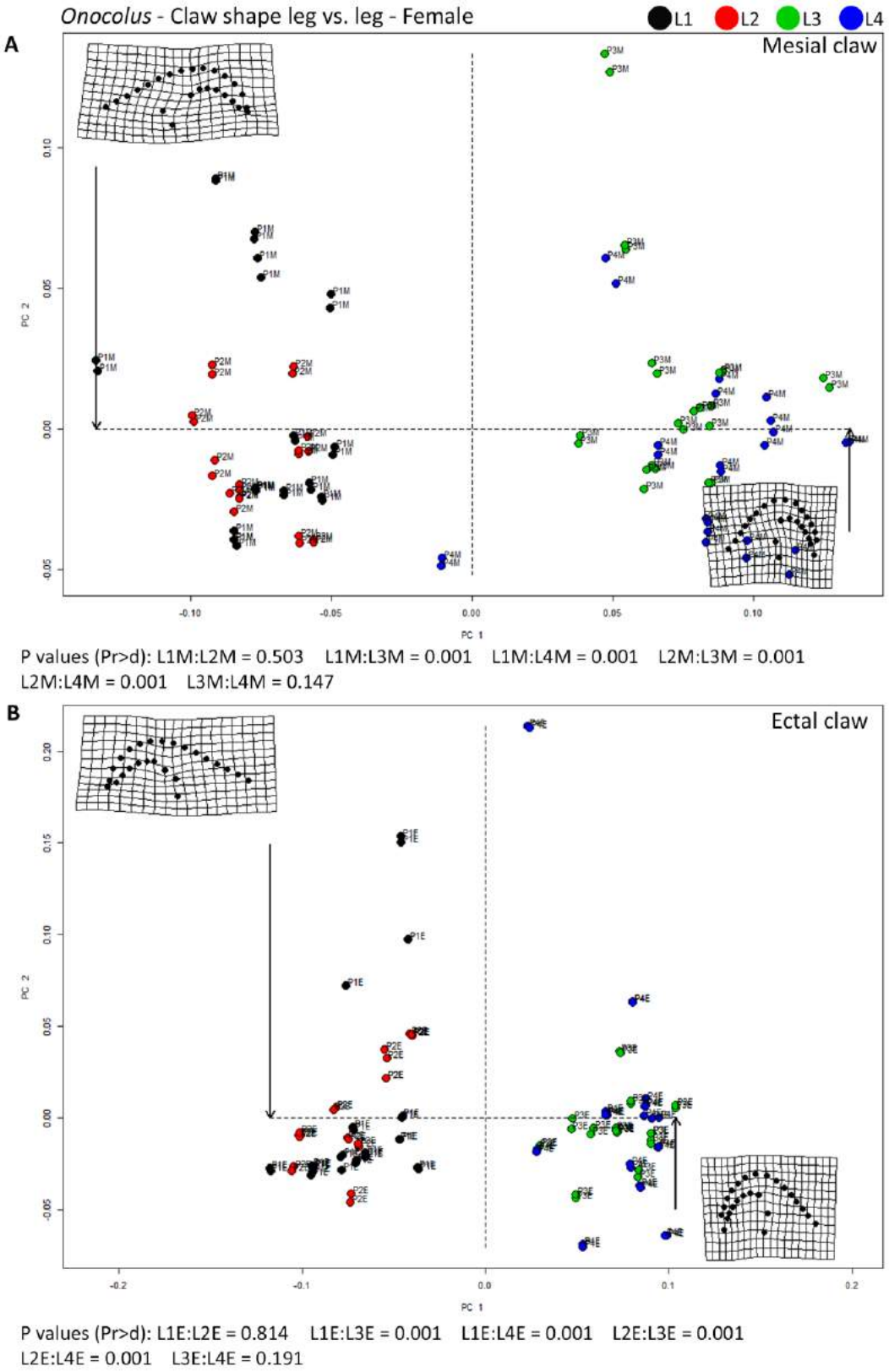
Graphic 8. Principal components analysis showing variation in homologous claws between legs in males of *Epicadus*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



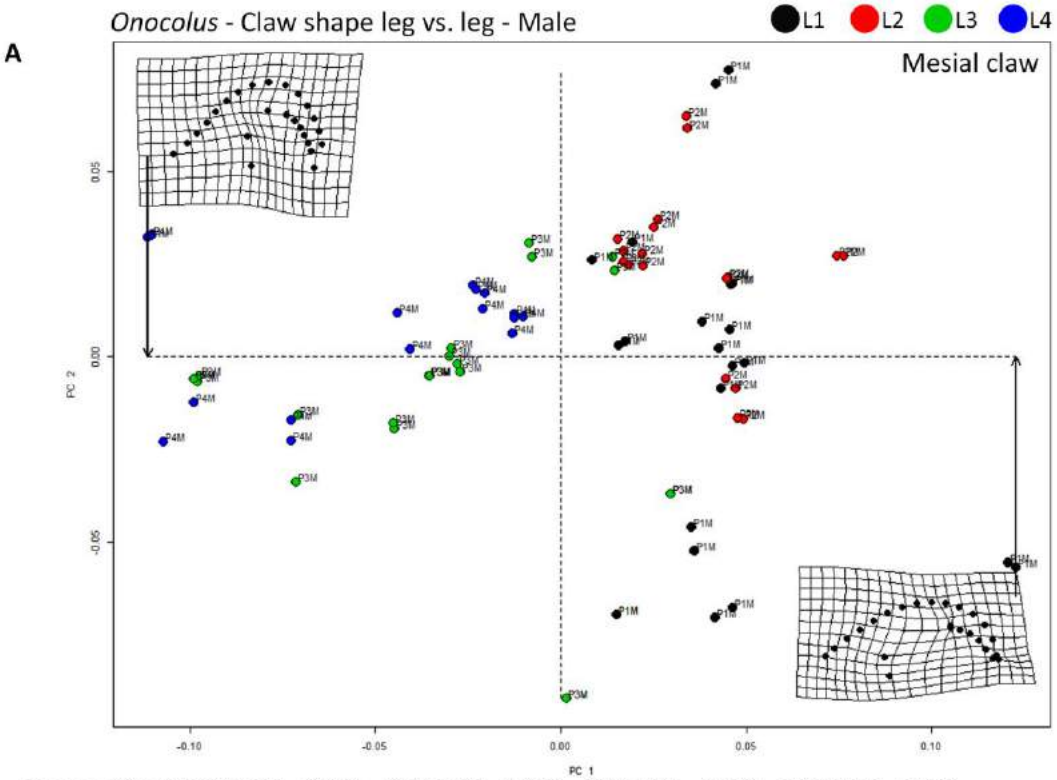
Graphic 9. Principal components analysis showing variation in homologous claws between legs in females of *Misumenops*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



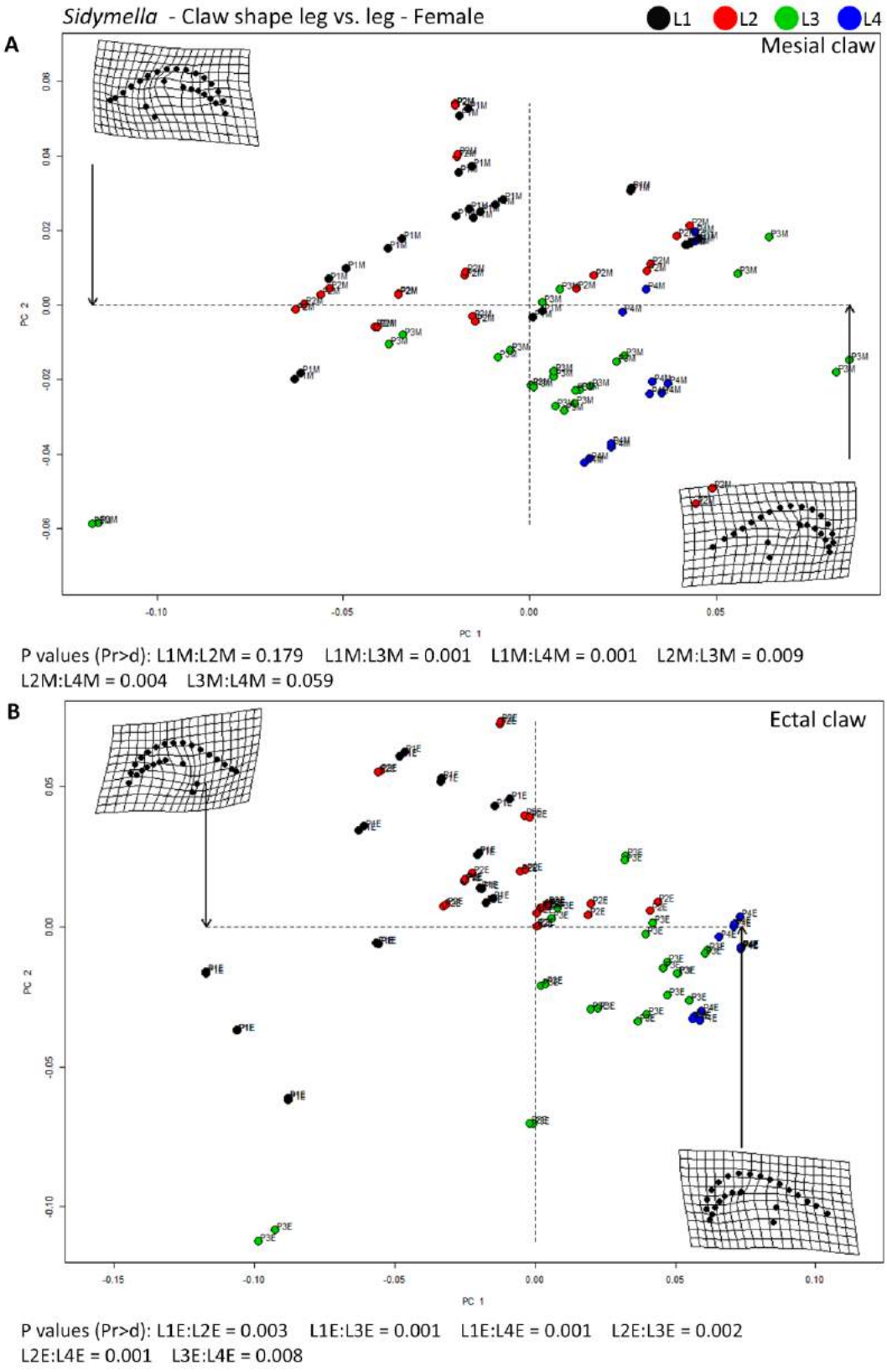
Graphic 10. Principal components analysis showing variation in homologous claws between legs in males of *Misumenops*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



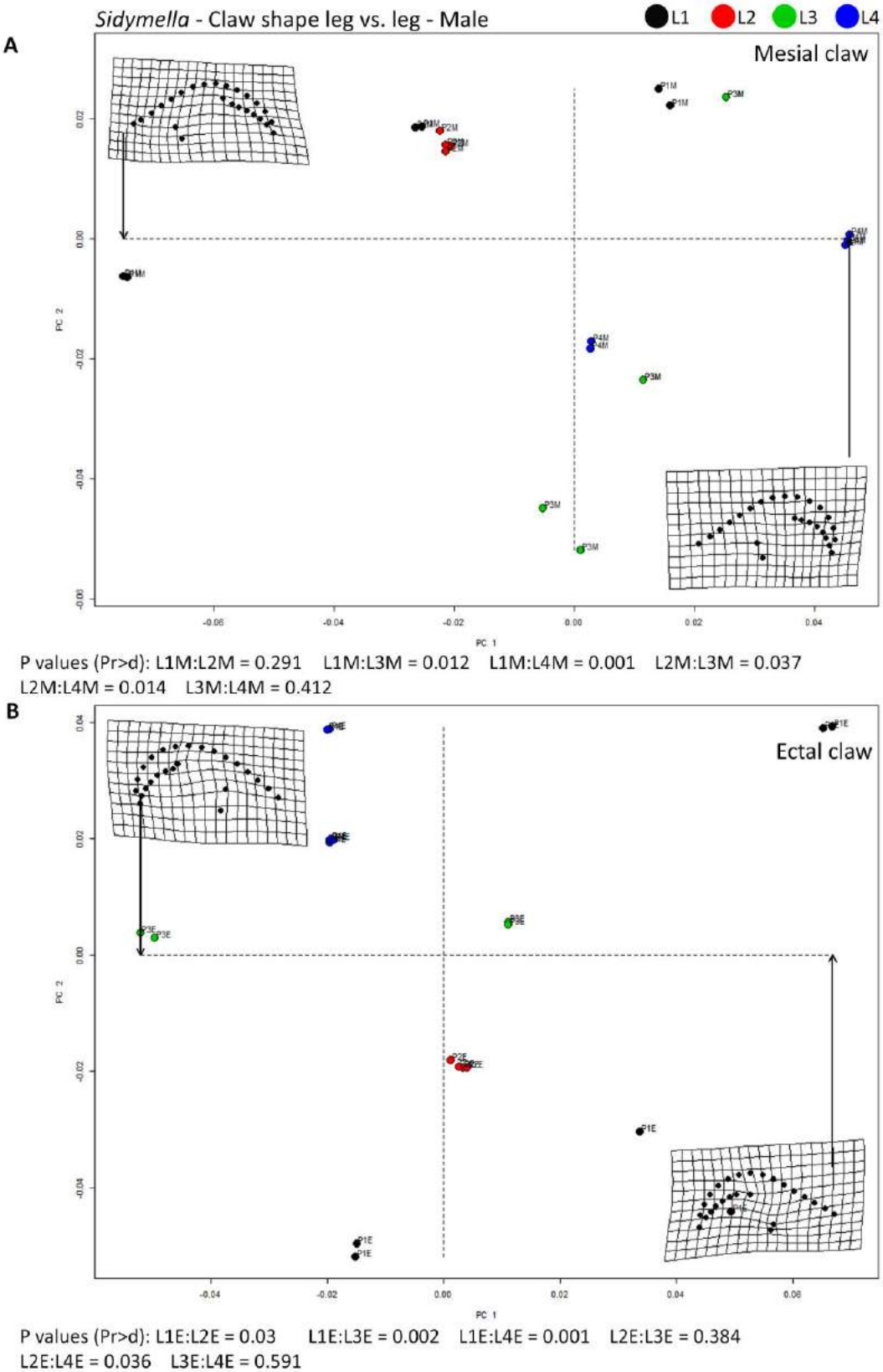
Graphic 11. Principal components analysis showing variation in homologous claws between legs in females of *Onocolus*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



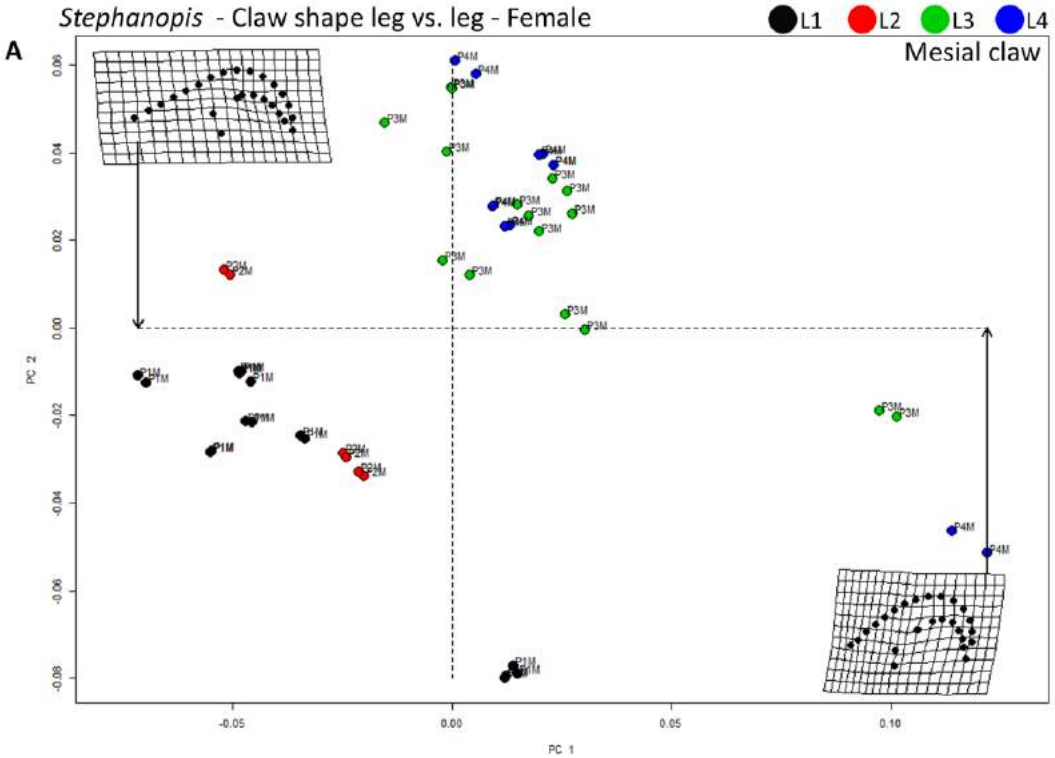
Graphic 12. Principal components analysis showing variation in homologous claws between legs in males of *Onocolus.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



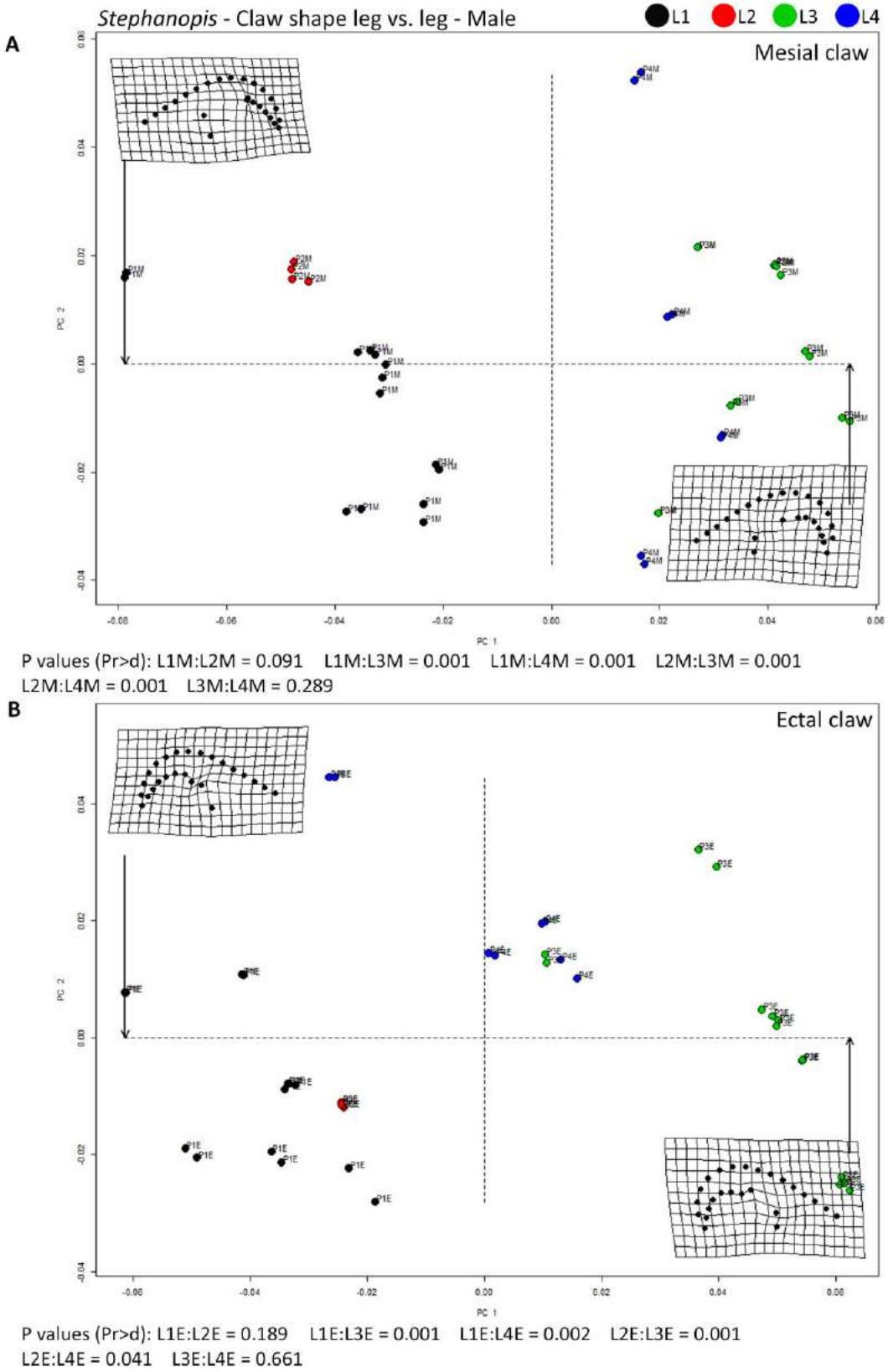
Graphic 13. Principal components analysis showing variation in homologous claws between legs in females of *Sidymella.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



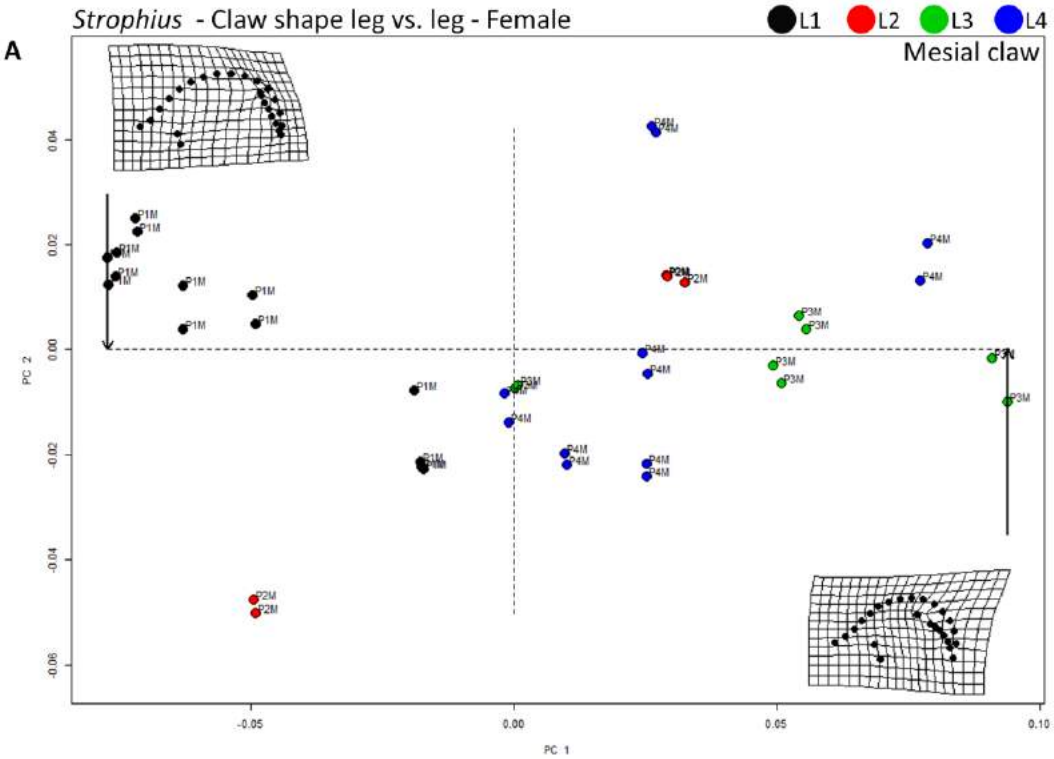
Graphic 14. Principal components analysis showing variation in homologous claws between legs in male of *Sidymella.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



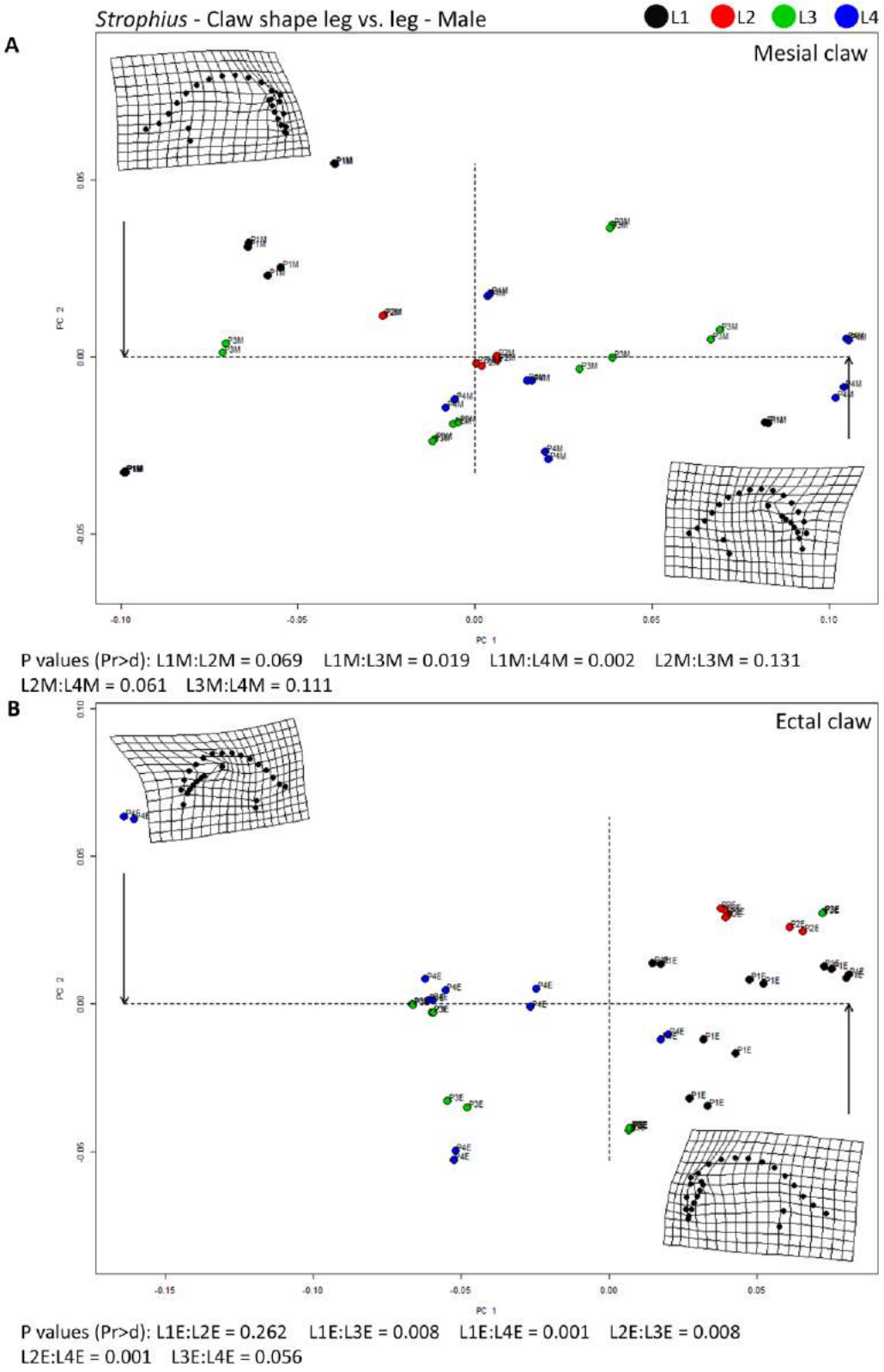
Graphic 15. Principal components analysis showing variation in homologous claws between legs in female of *Stephanopis*. P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



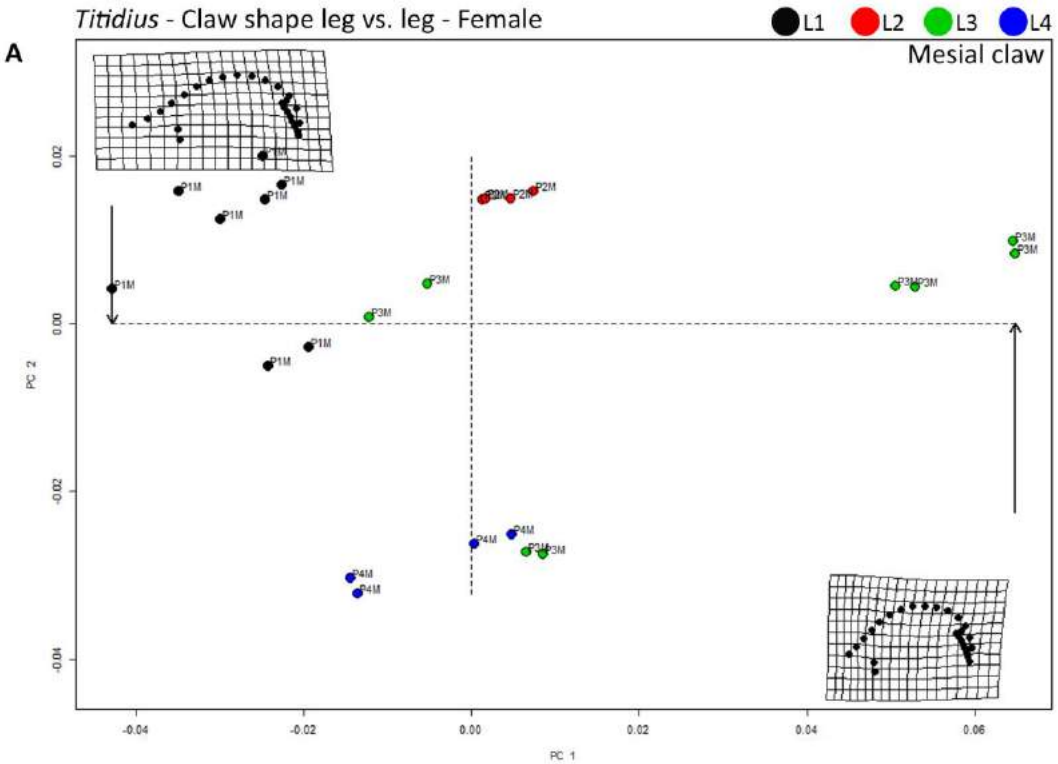
Graphic 16. Principal components analysis showing variation in homologous claws between legs in male of *Stephanopis.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



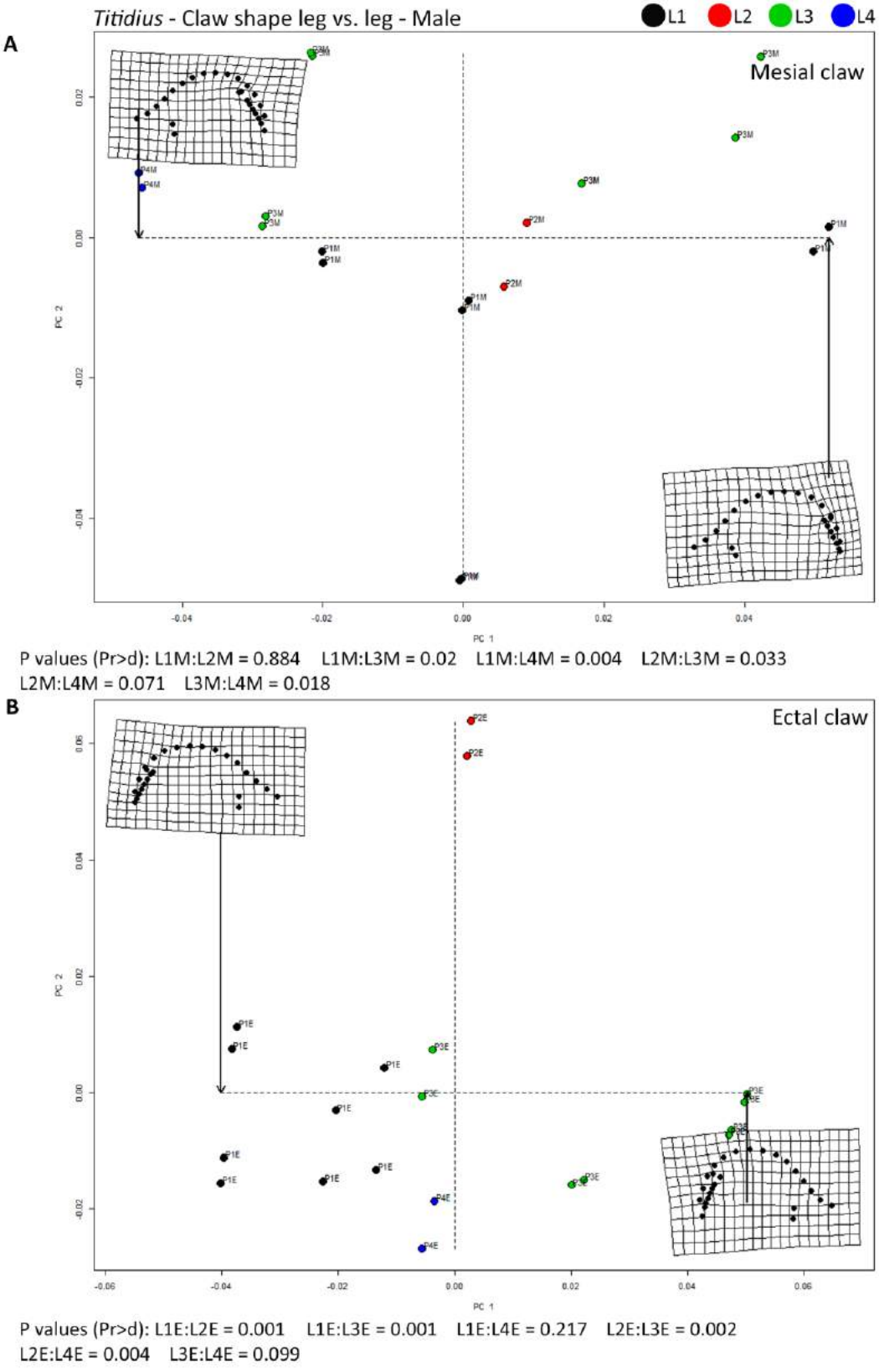
Graphic 17. Principal components analysis showing variation in homologous claws between legs in female of *Strophius.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



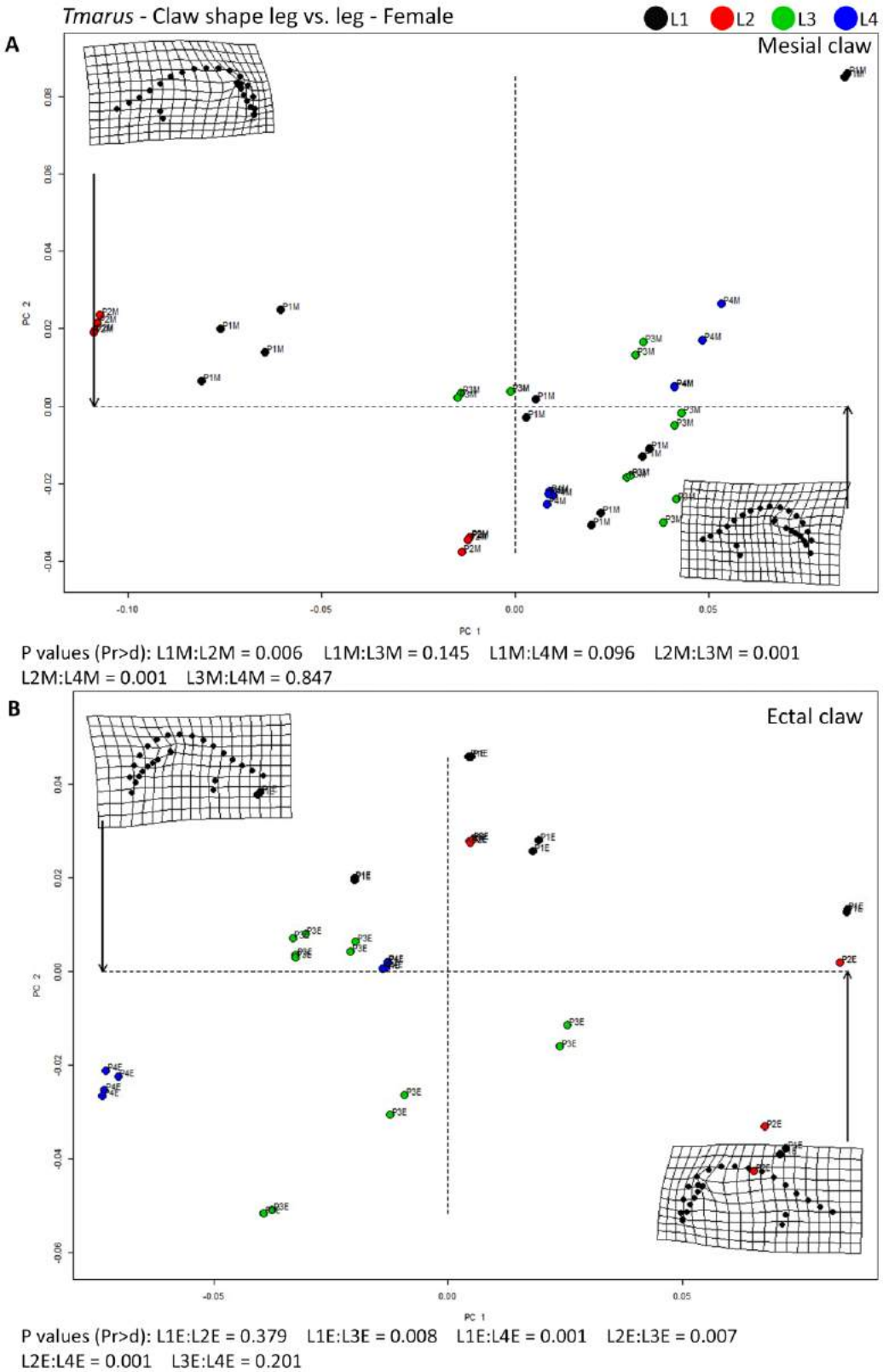
Graphic 18. Principal components analysis showing variation in homologous claws between legs in male of *Strophius.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



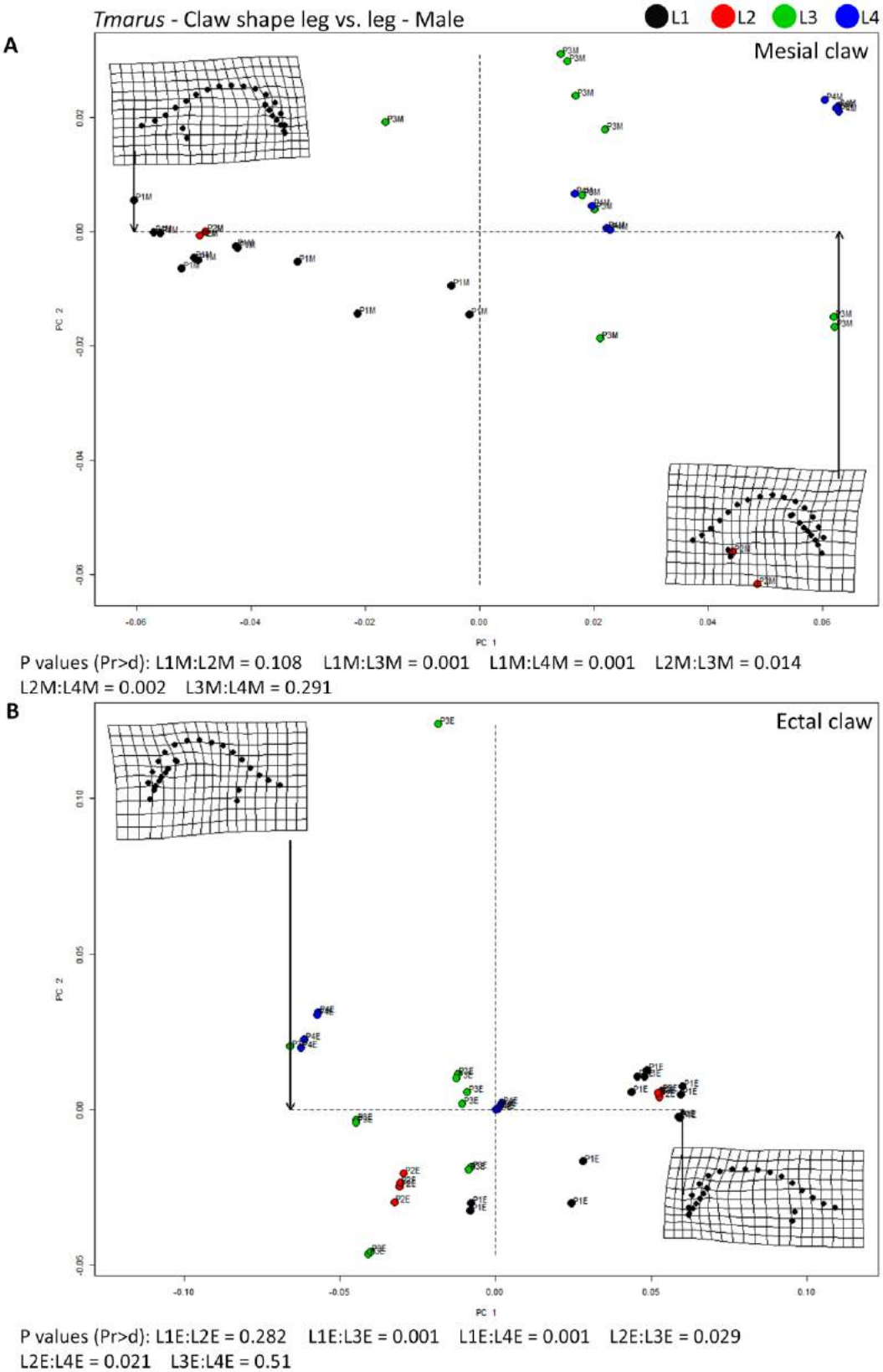
Graphic 19. Principal components analysis showing variation in homologous claws between legs in female of *Titidius.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



Graphic 20. Principal components analysis showing variation in homologous claws between legs in male of *Titidius.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



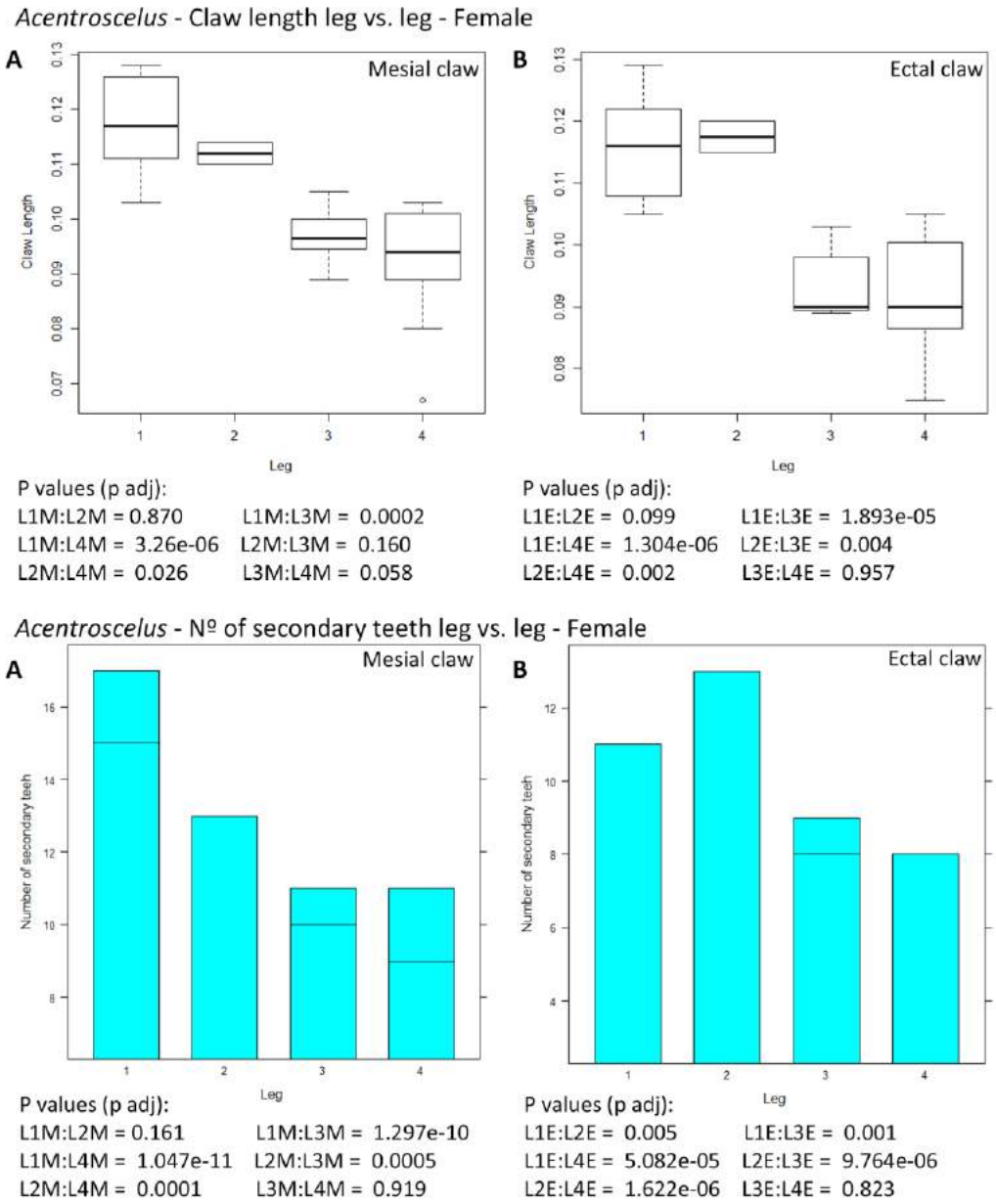
Graphic 21. Principal components analysis showing variation in homologous claws between legs in female of *Tmarus.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively



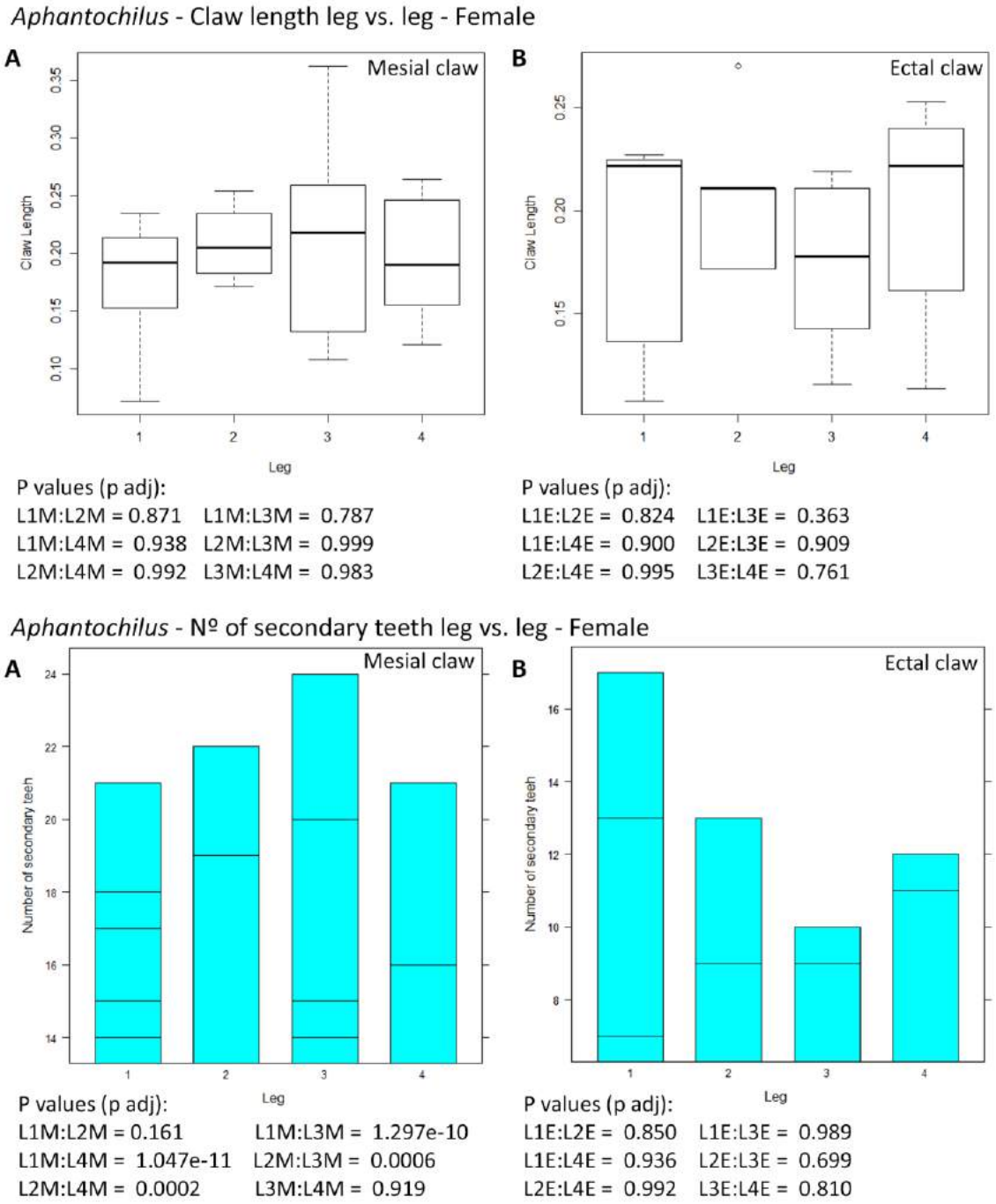
Graphic 22. Principal components analysis showing variation in homologous claws between legs in male of *Tmarus.* P-values of MANOVA pairwise comparisons are provided below graphic. (A) Comparison of mesial claws (B) Comparison of ectal claws. Points in grids in top left corner and bottom right corner illustrate vector diagrams of maximum shape variance in pc1 and pc2 respectively

APPENDIX 6

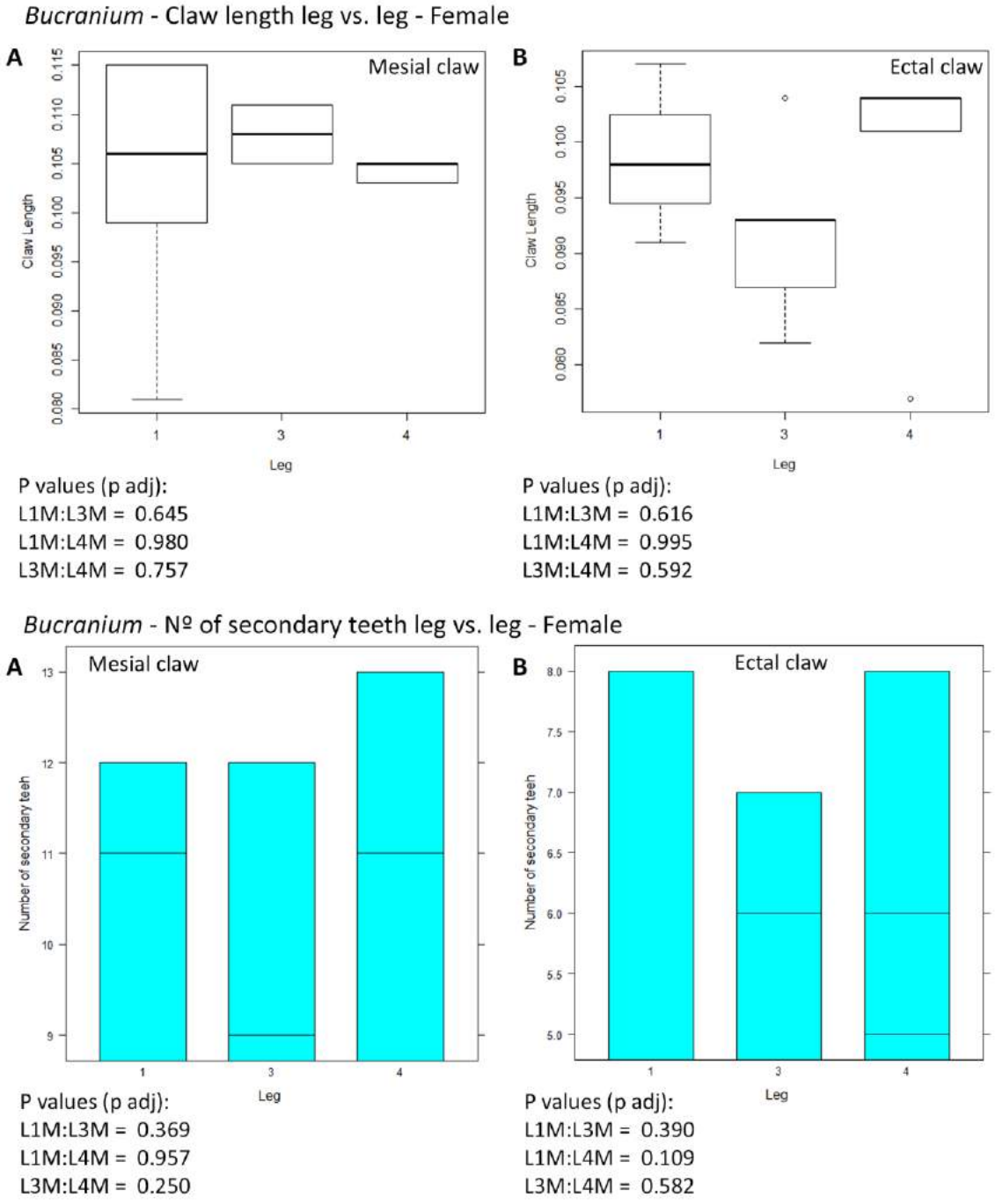
Boxplots and Bar plotsillustrating the claws' length and number of teeth in each analyzed genus, with the p values of THSD tests bellow. Box plots are displaying displaying minimum, first quartile, second quartile (median), third quartile and maximum. Horizontal line in bar plots represent absolute values.



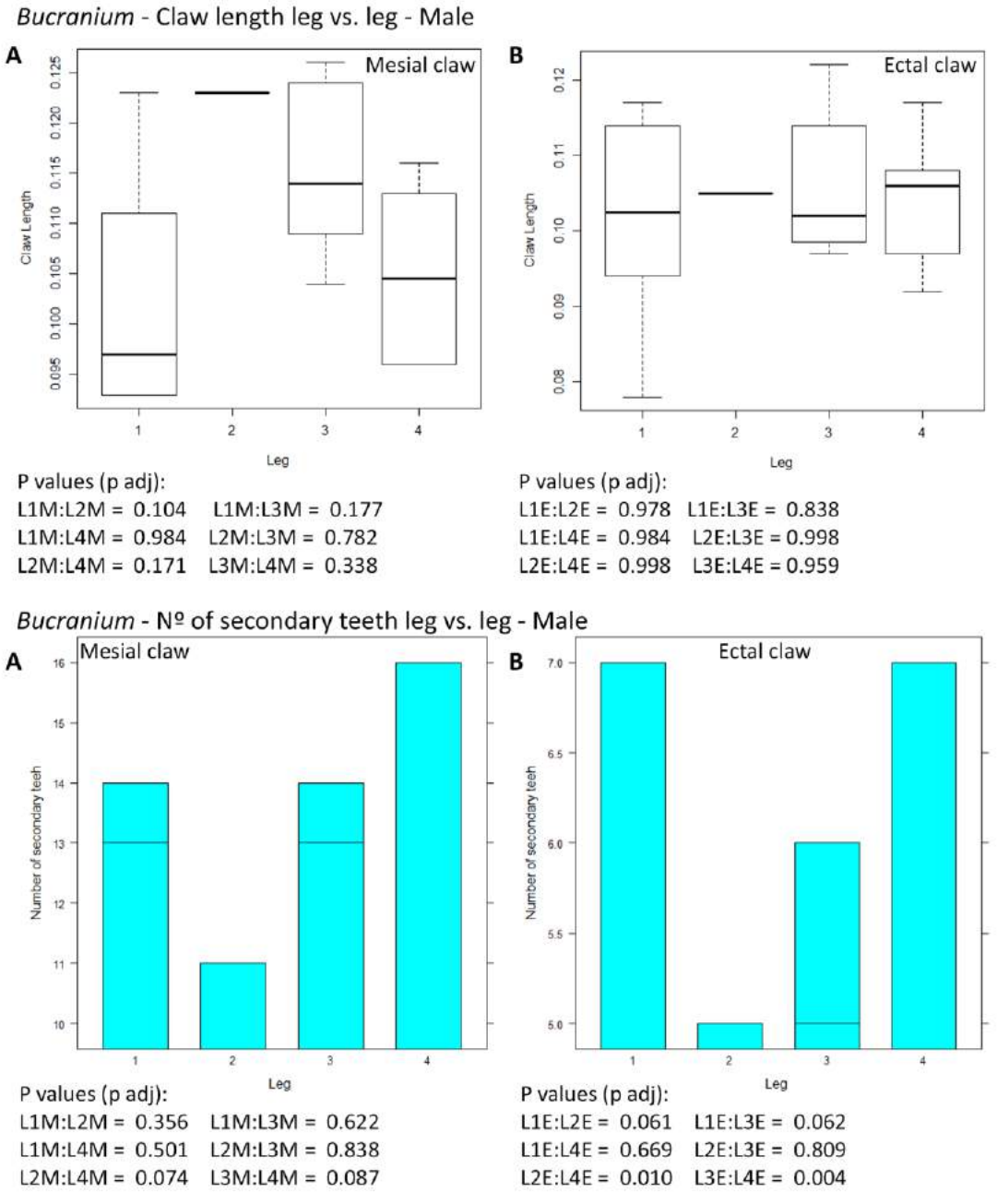
Graphic 1 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Acentroscelus.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Acentroscelus.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In females of *Acentroscelus*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Acentroscelus*.



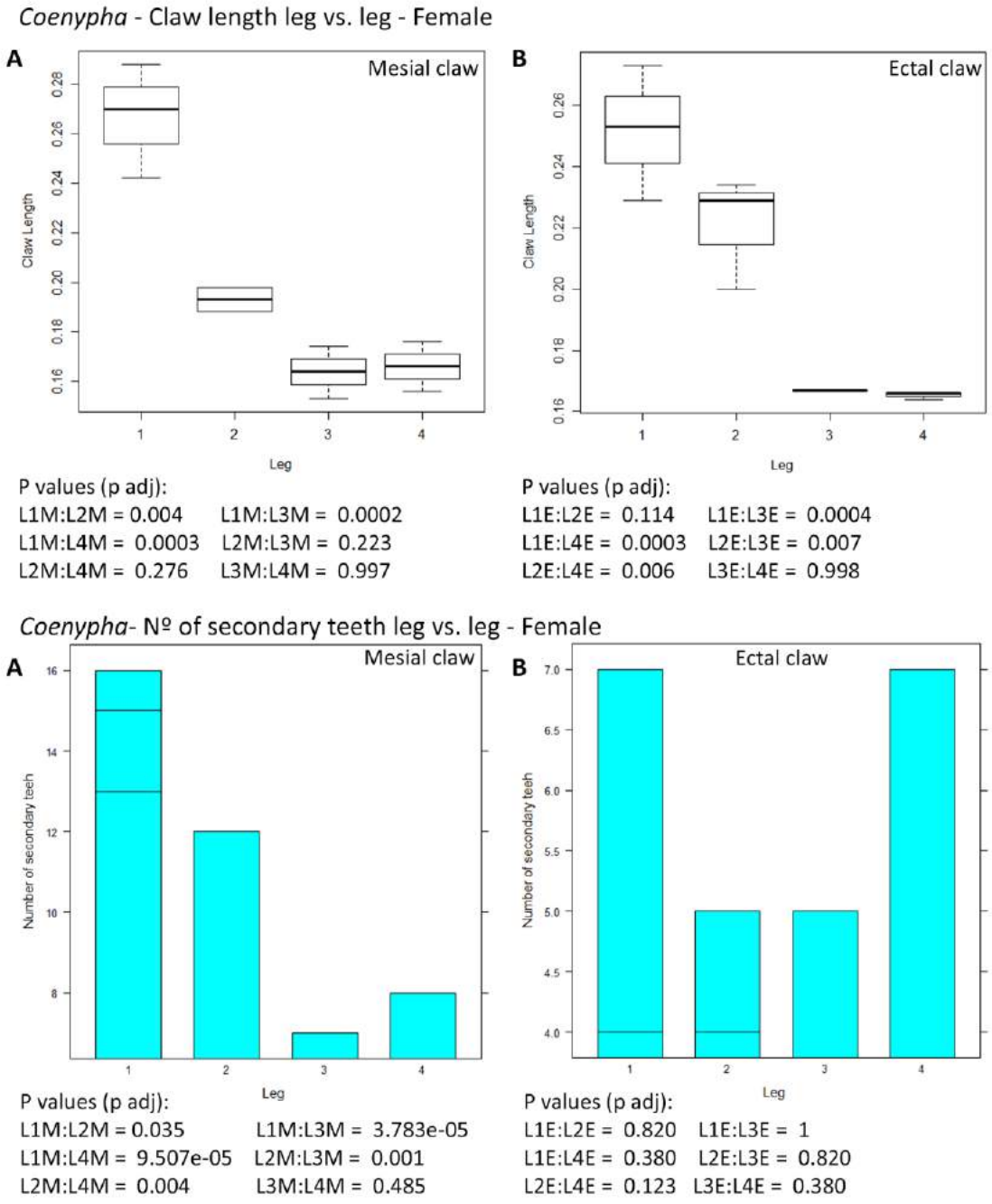
Graphic 2 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Aphantochilus.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Aphantochilus.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In females of *Aphantochilus*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Aphantochilus*.



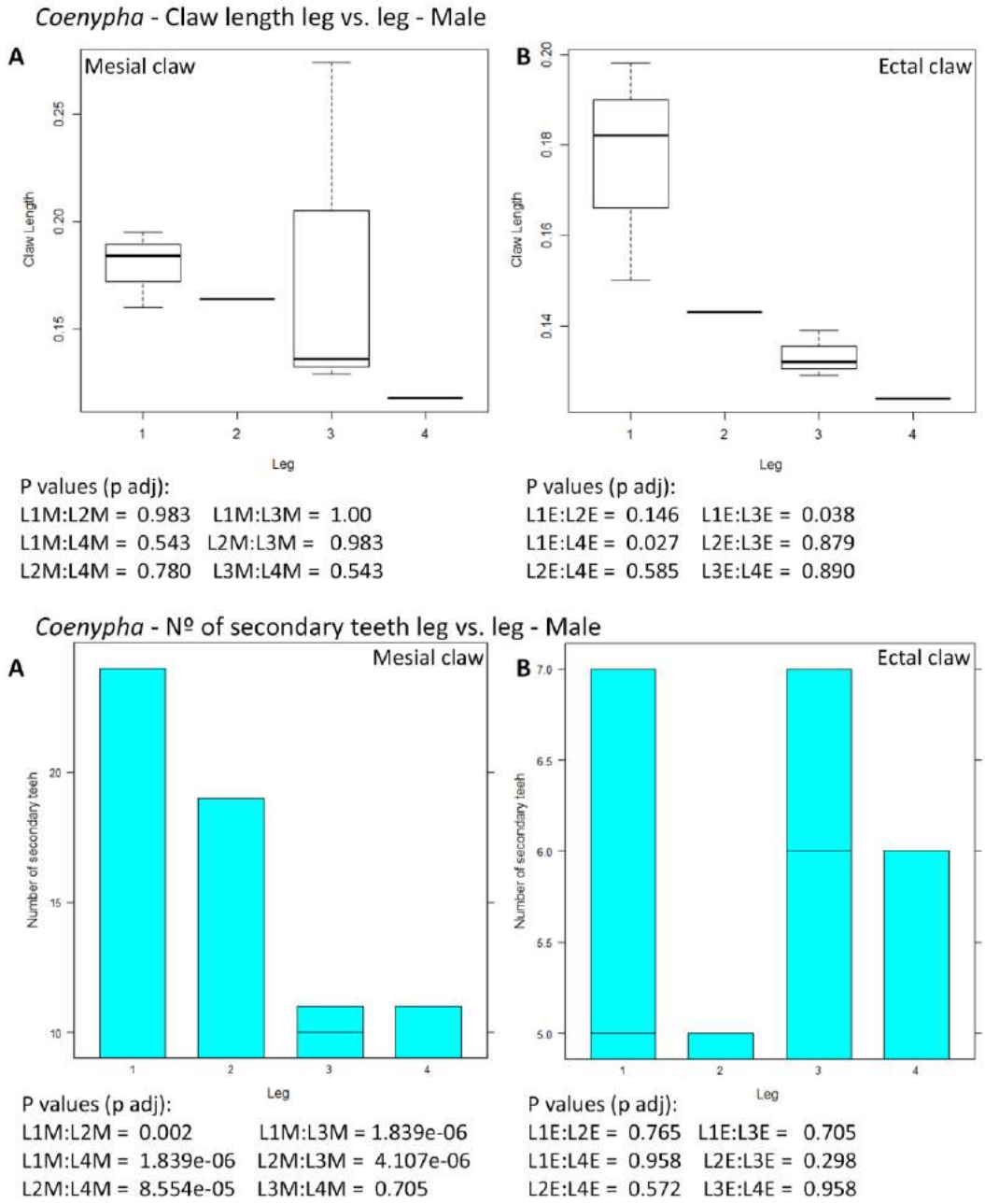
Graphic 3 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Bucranium.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Bucranium.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In females of *Bucranium*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Bucranium*.



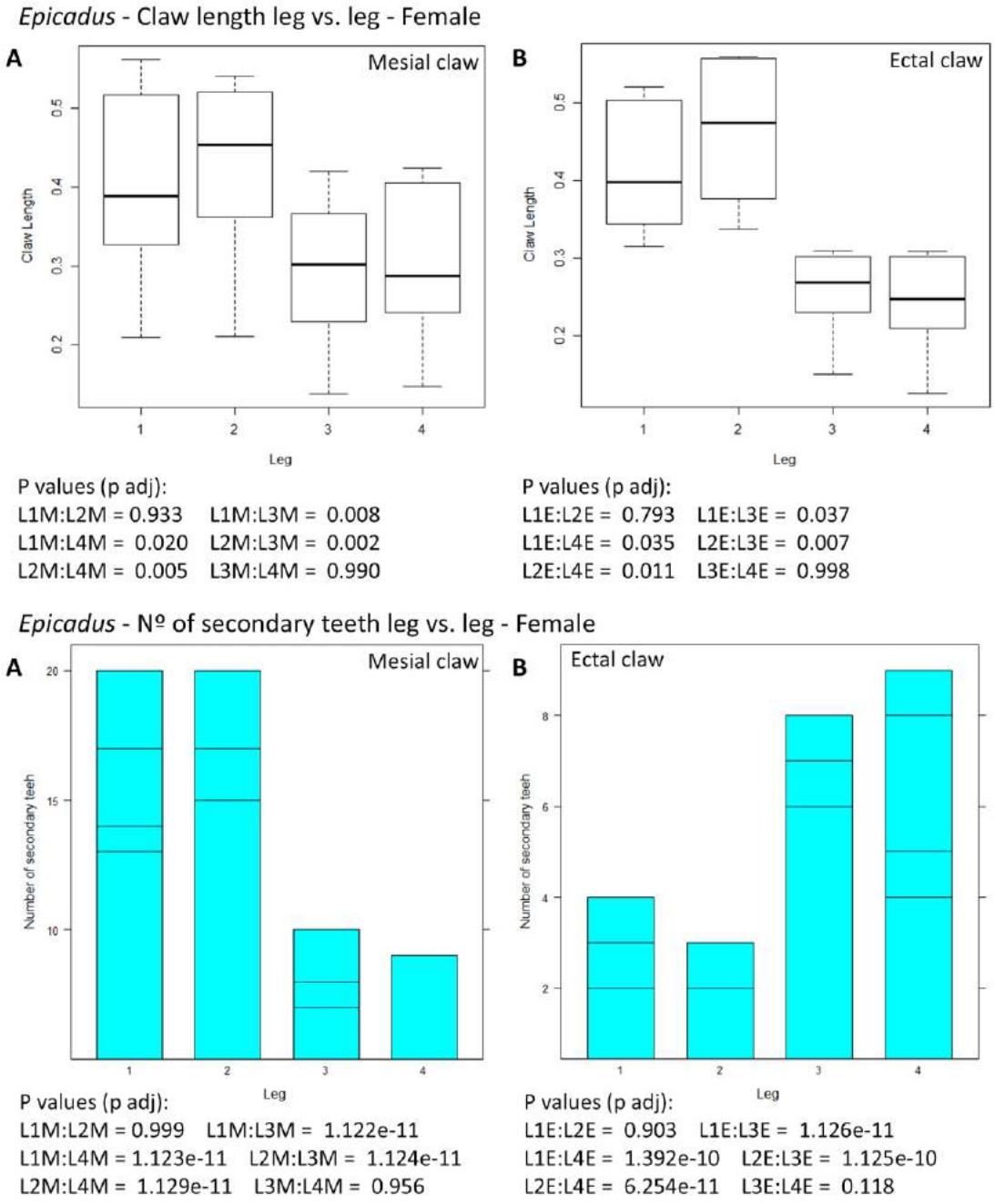
Graphic 4 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in male of *Bucranium.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in male of *Bucranium.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In male of *Bucranium*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in male of *Bucranium*.



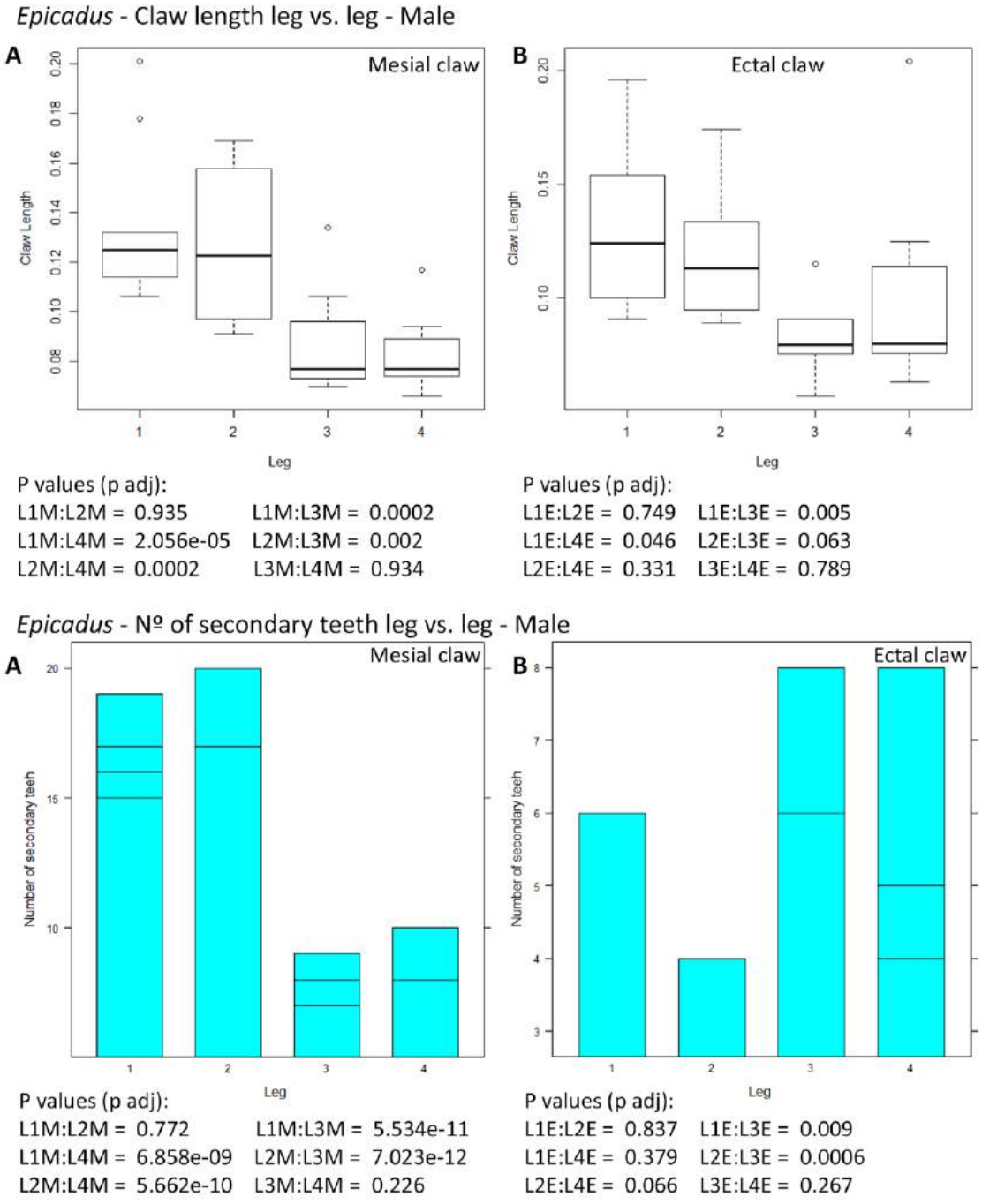
Graphic 5 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in female of *Coenypha.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in male of *Coenypha.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In female of *Coenypha*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in female of *Coenypha*.



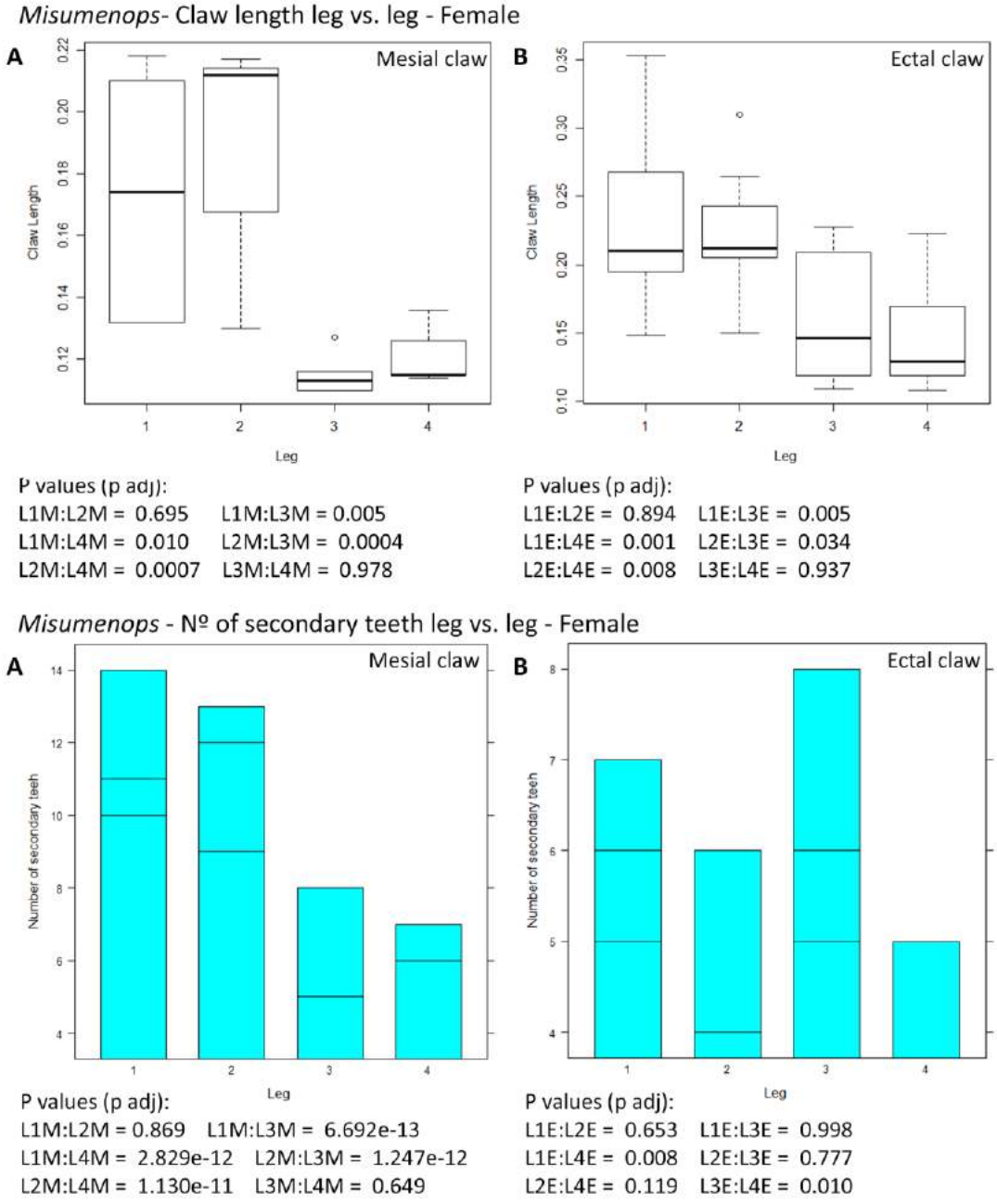
Graphic 6 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in male of *Coenypha.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in male of *Coenypha.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In male of *Coenypha*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in male of *Coenypha*.



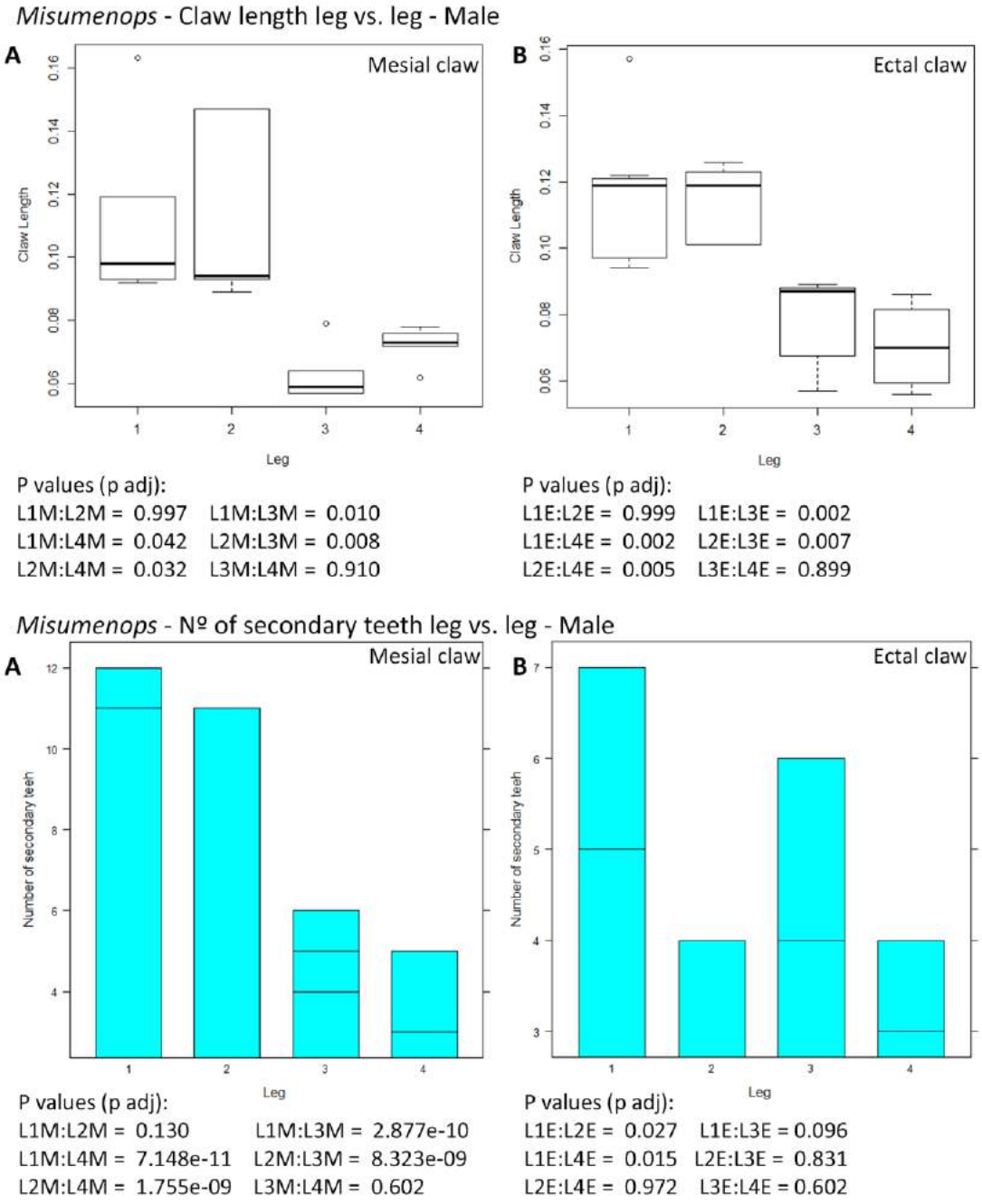
Graphic 7 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in female of *Epicadus.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in female of *Epicadus.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In female of *Epicadus*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in female of *Epicadus*.



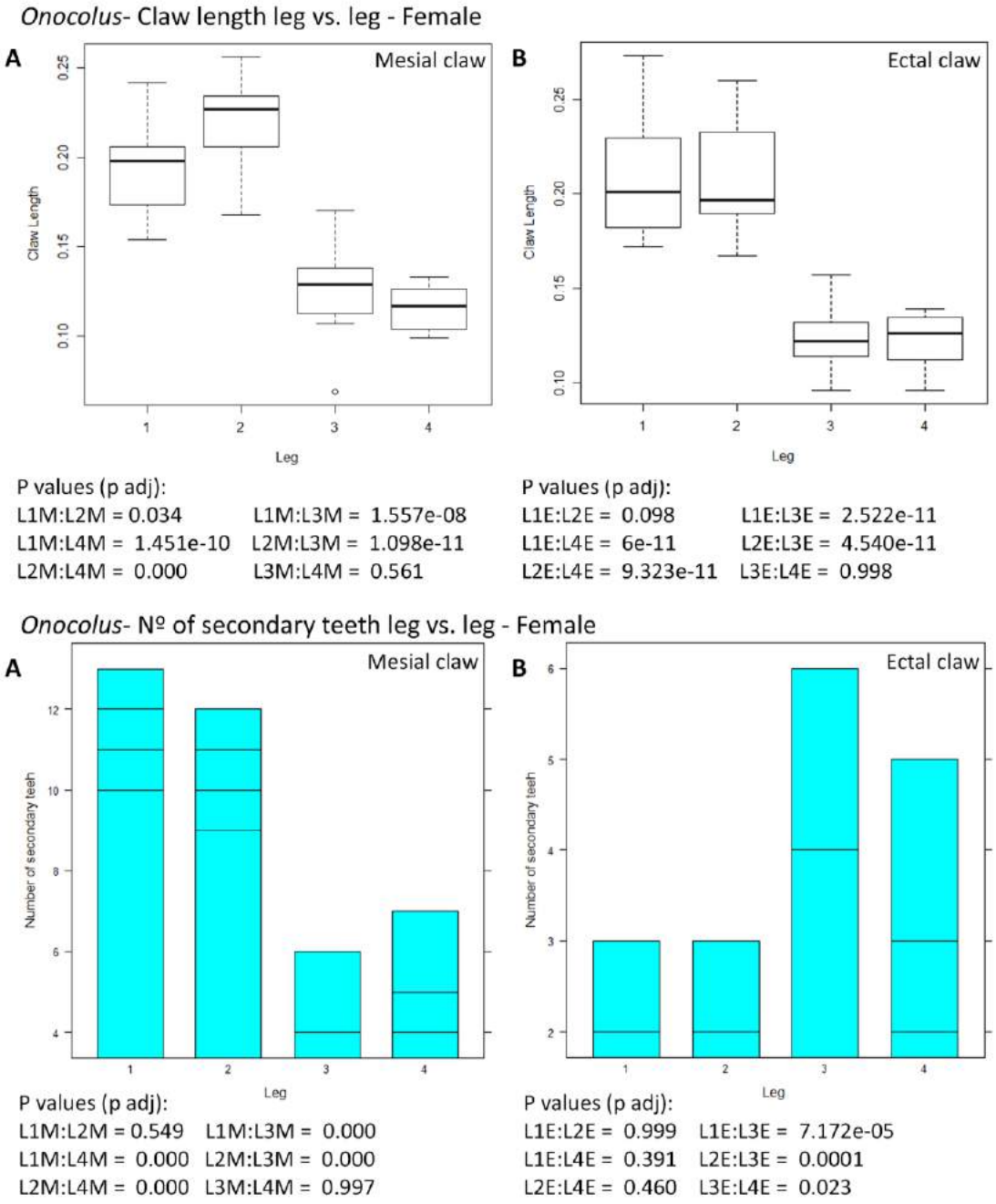
Graphic 8 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in male of *Epicadus.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in male of *Epicadus.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In male of *Epicadus*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in male of *Epicadus*.



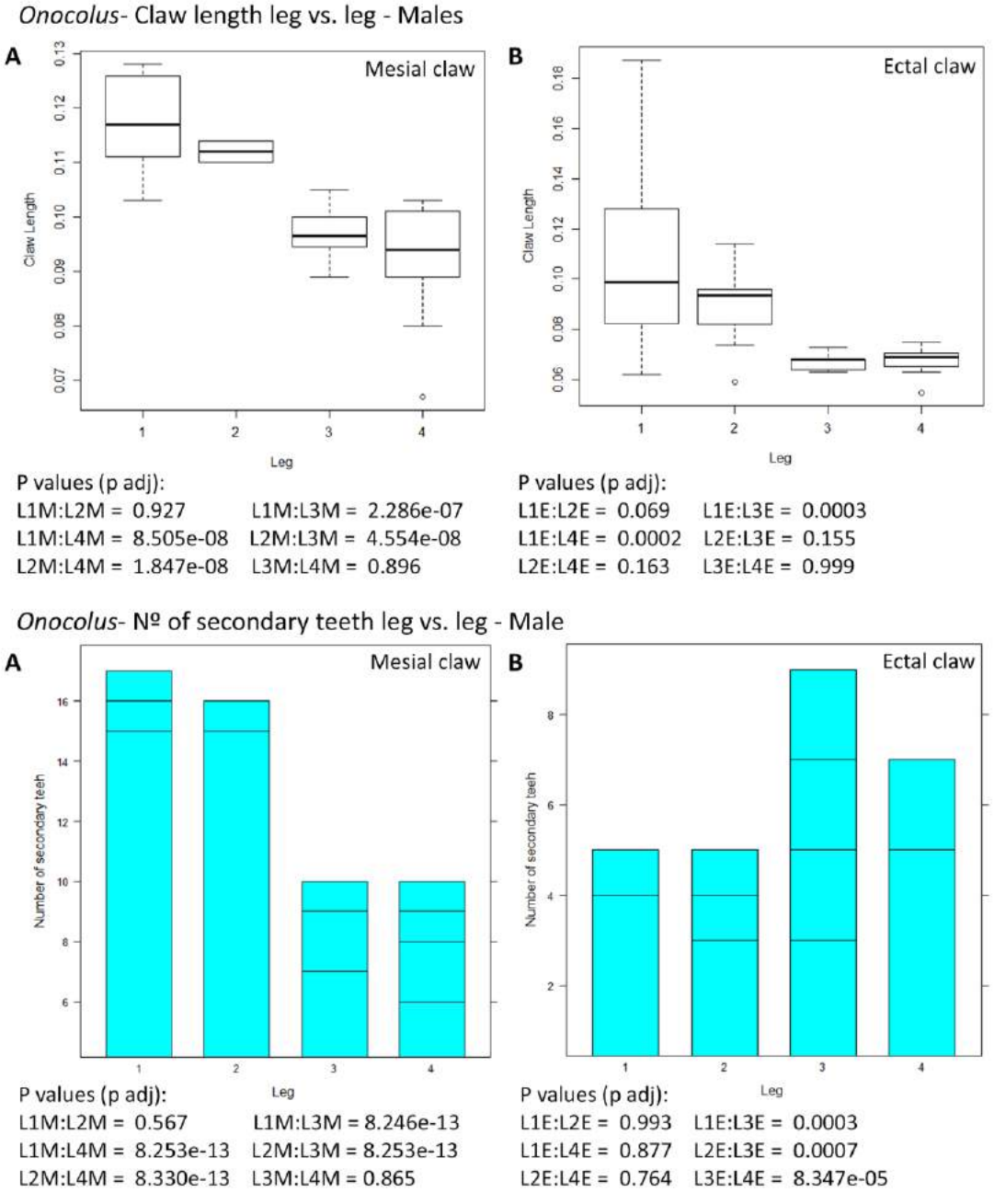
Graphic 9 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Misumenops.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Misumenops.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In females of *Misumenops*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Misumenops*.



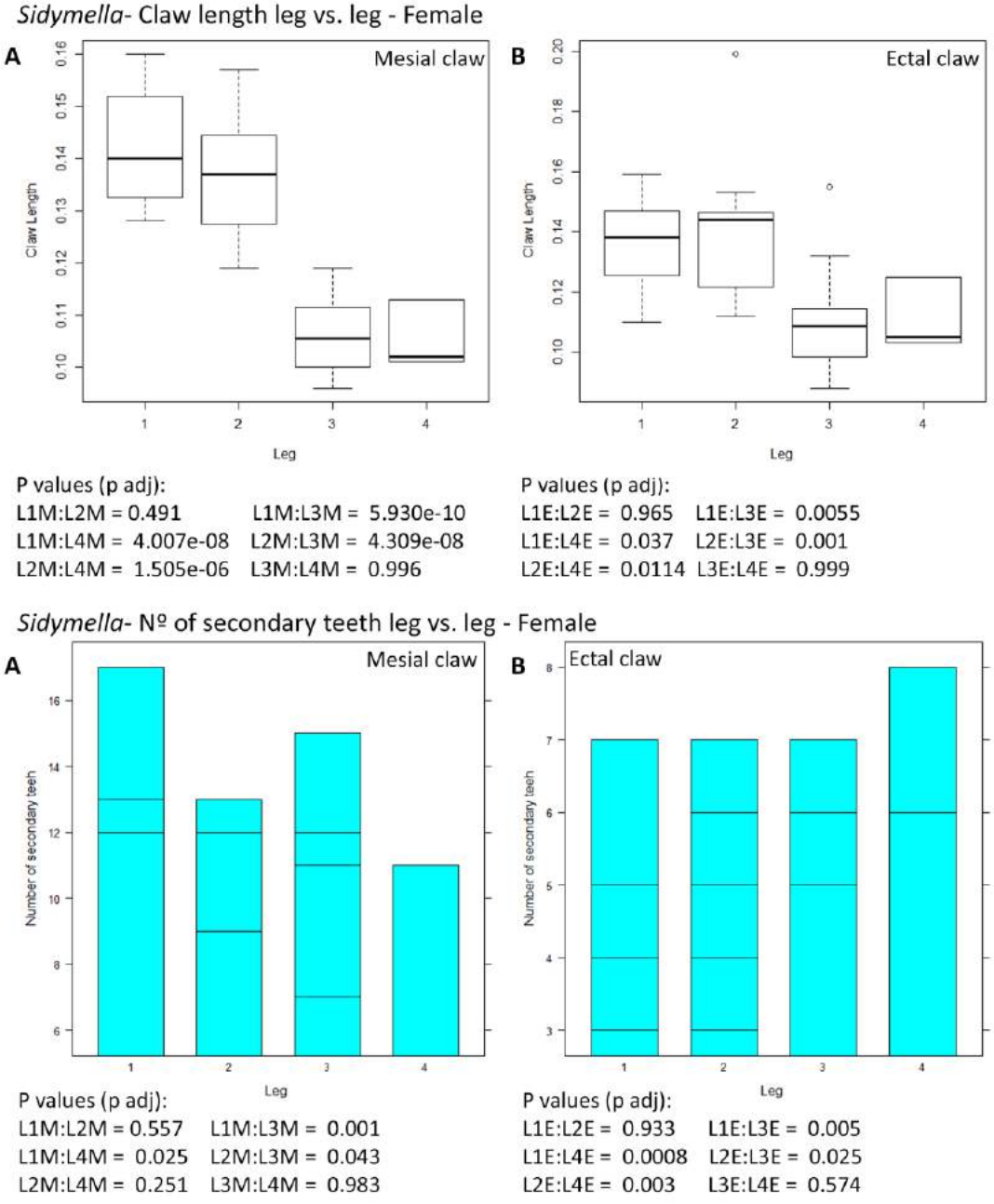
Graphic 10 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in male of *Misumenops.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in males of *Misumenops.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In males of *Misumenops*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in males of *Misumenops*.



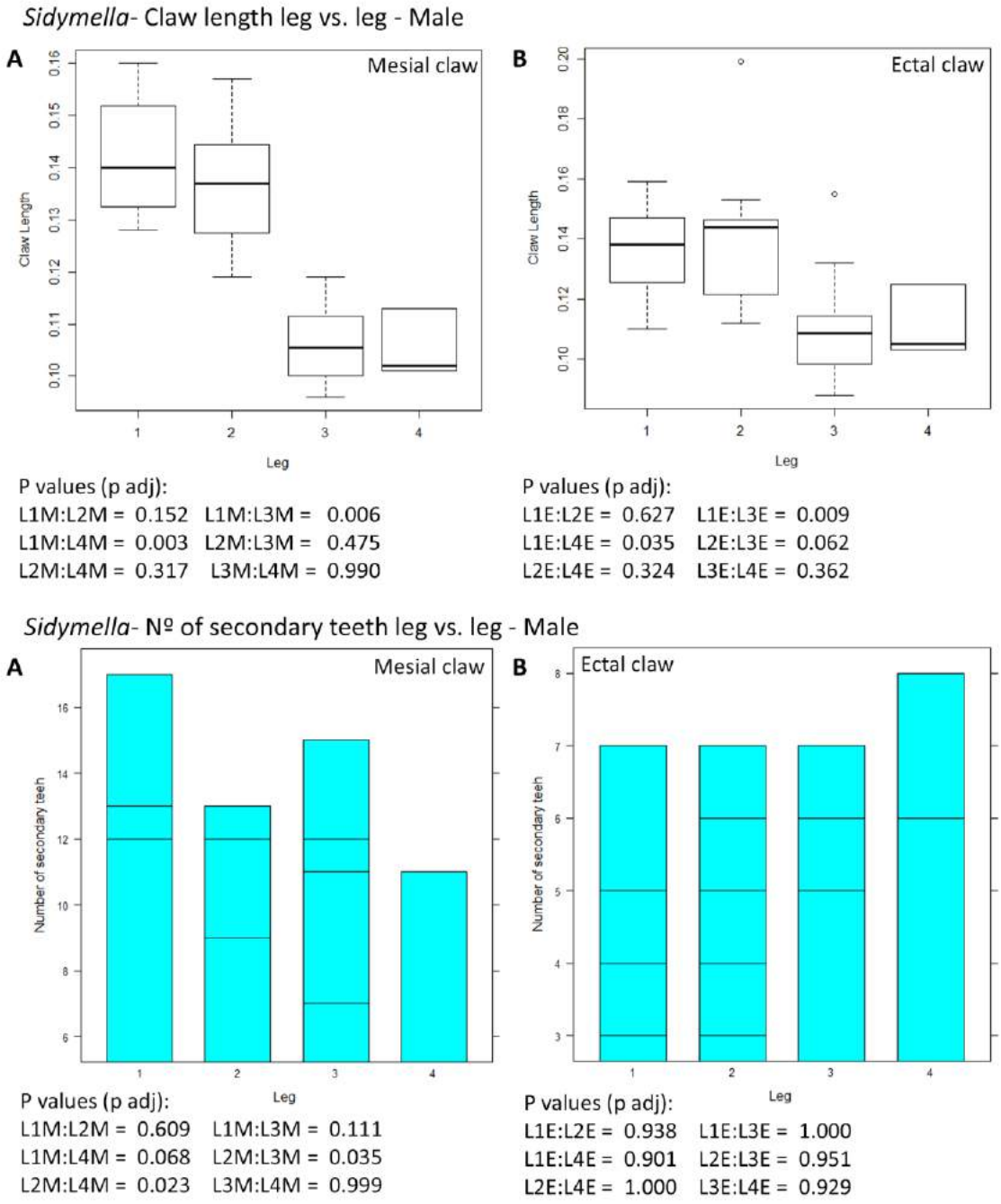
Graphic 11 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Onocolus.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Onocolus.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In males of *Onocolus*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Onocolus*.



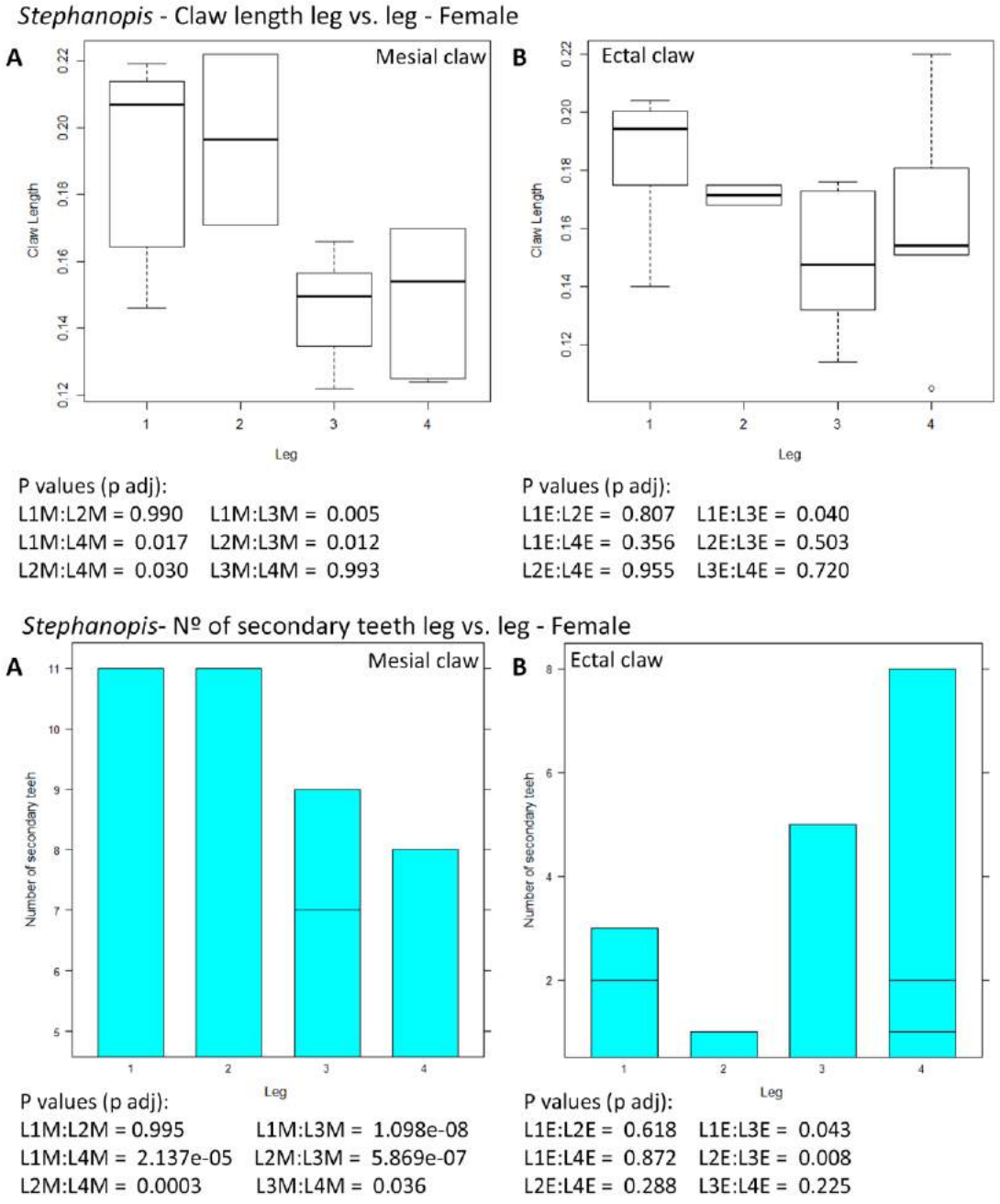
Graphic 12 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in males of *Onocolus.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in males of *Onocolus.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In males of *Onocolus*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in males of *Onocolus*.



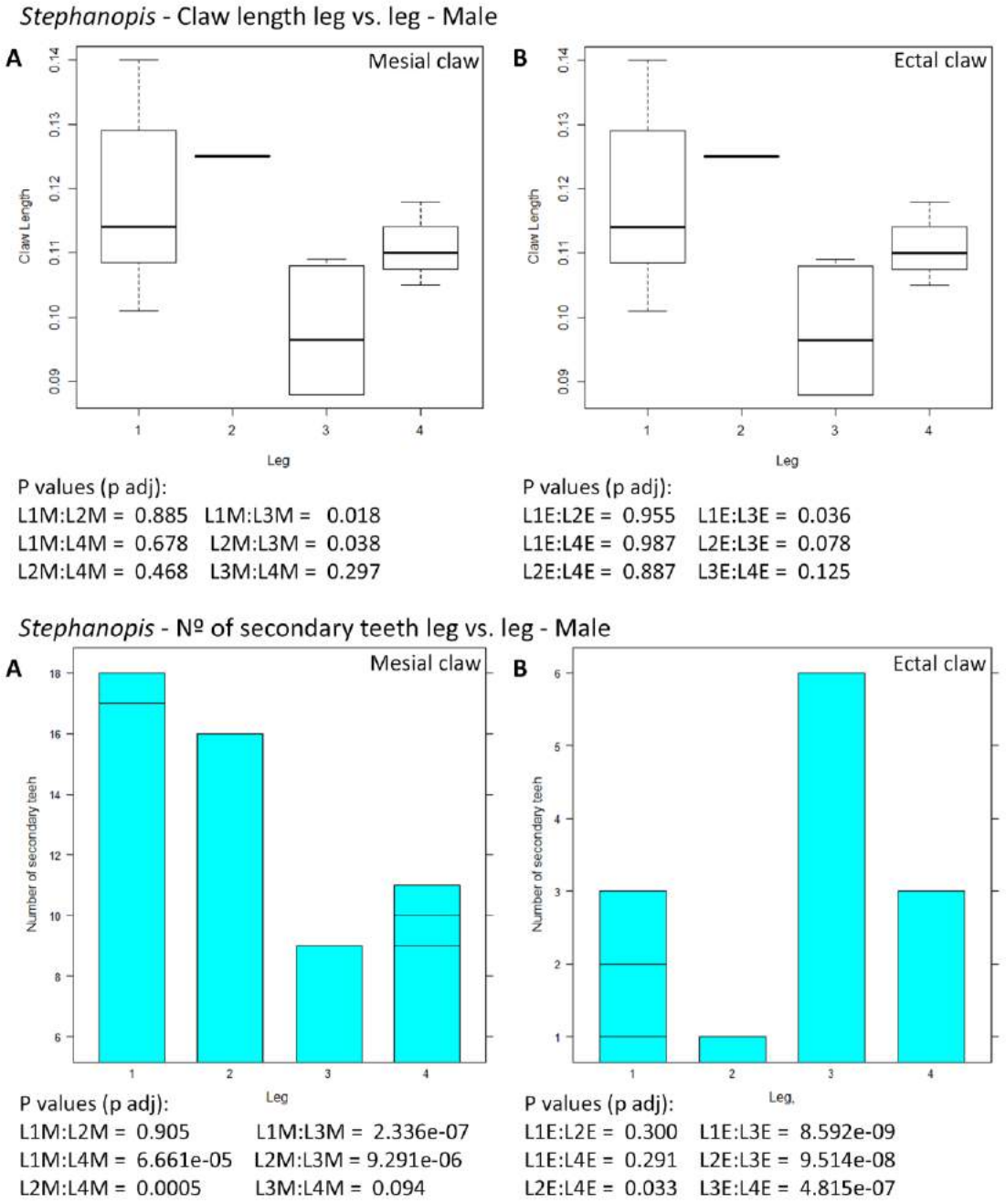
Graphic 13 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Sidymella.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Sidymella.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In females of *Sidymella*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Sidymella*.



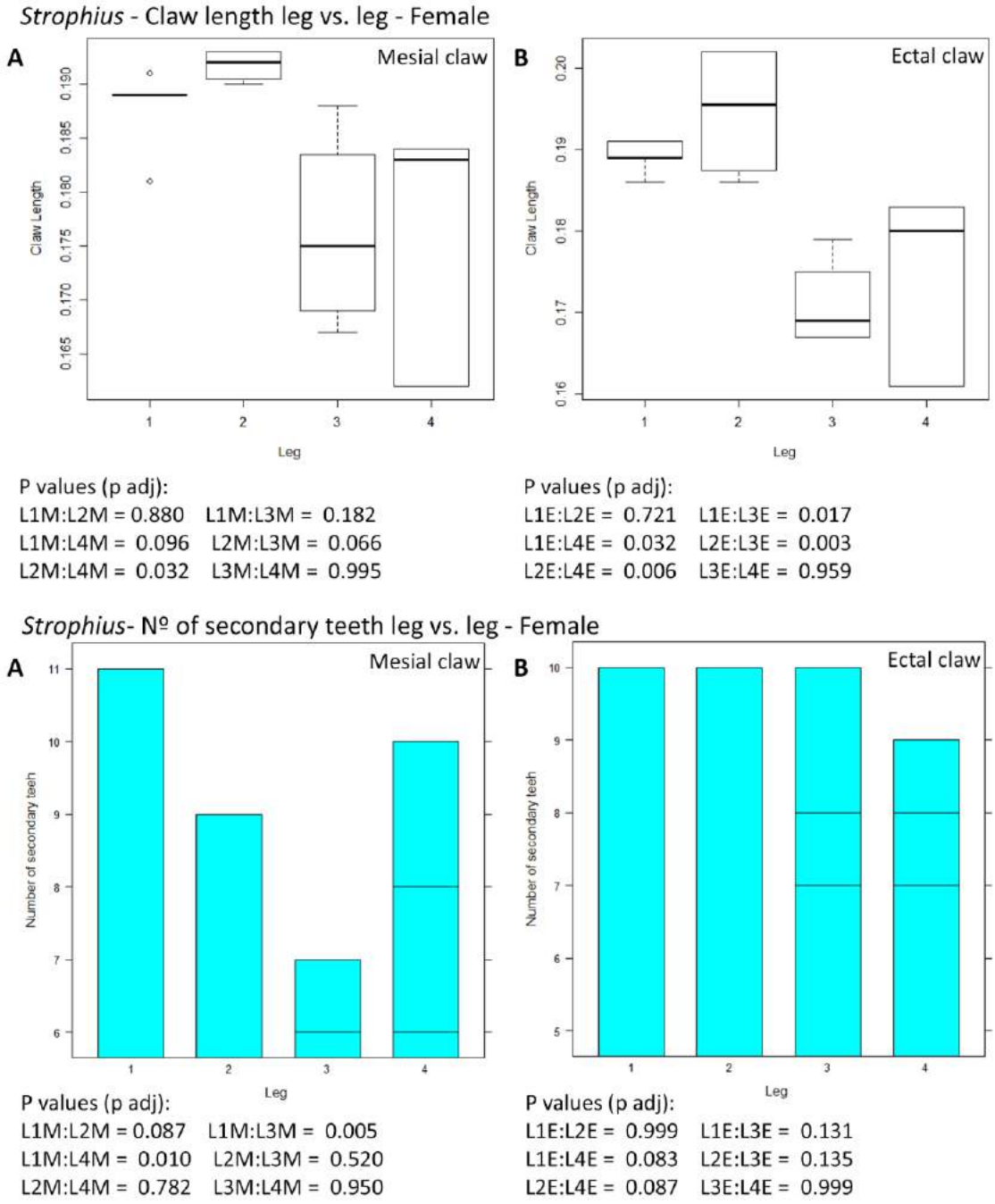
Graphic 13 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in males of *Sidymella.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Sidymella.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In males of *Sidymella*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in males of *Sidymella*.



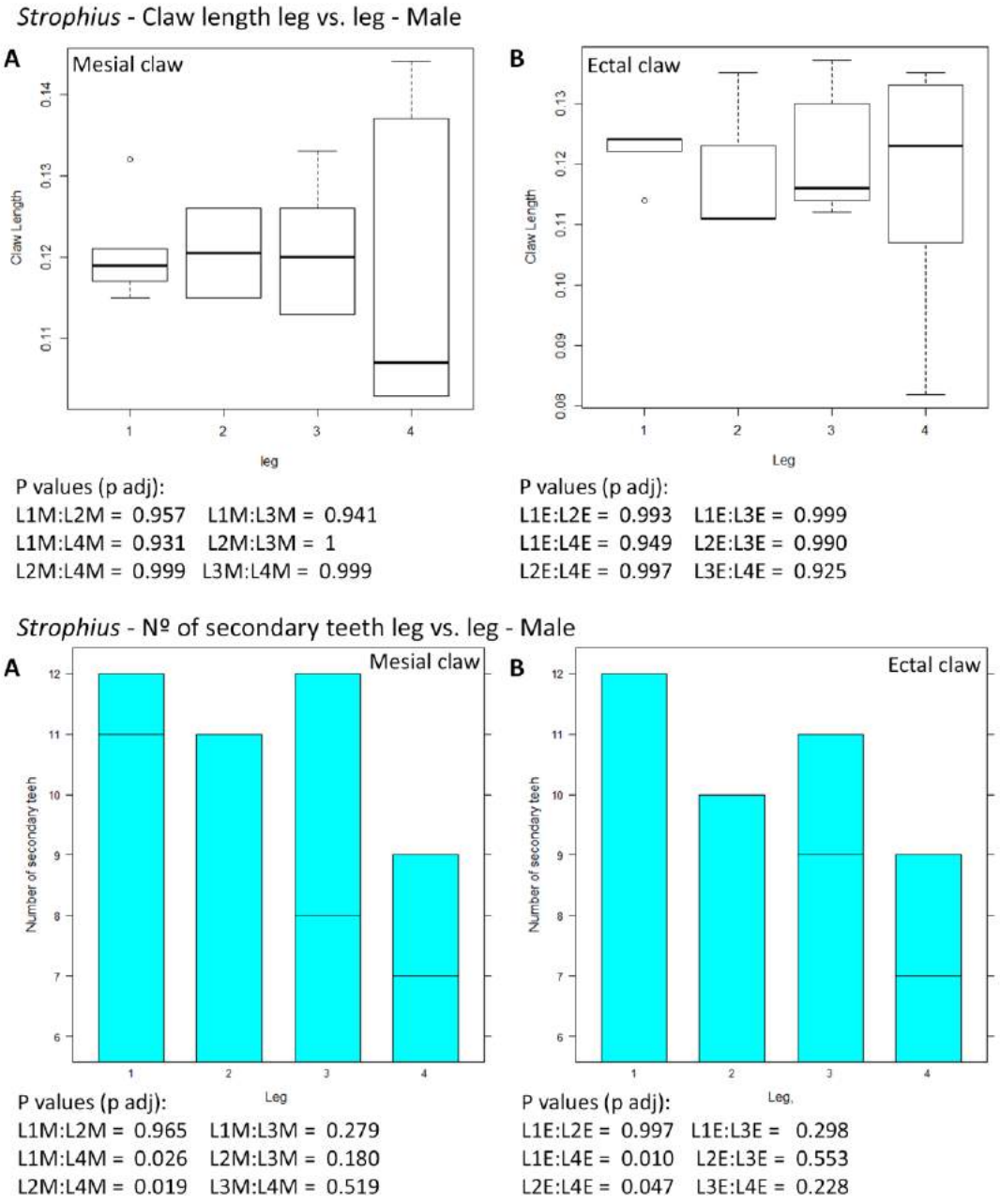
Graphic 15 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Strophius.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Strophius.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In females of *Strophius* (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Strophius*.



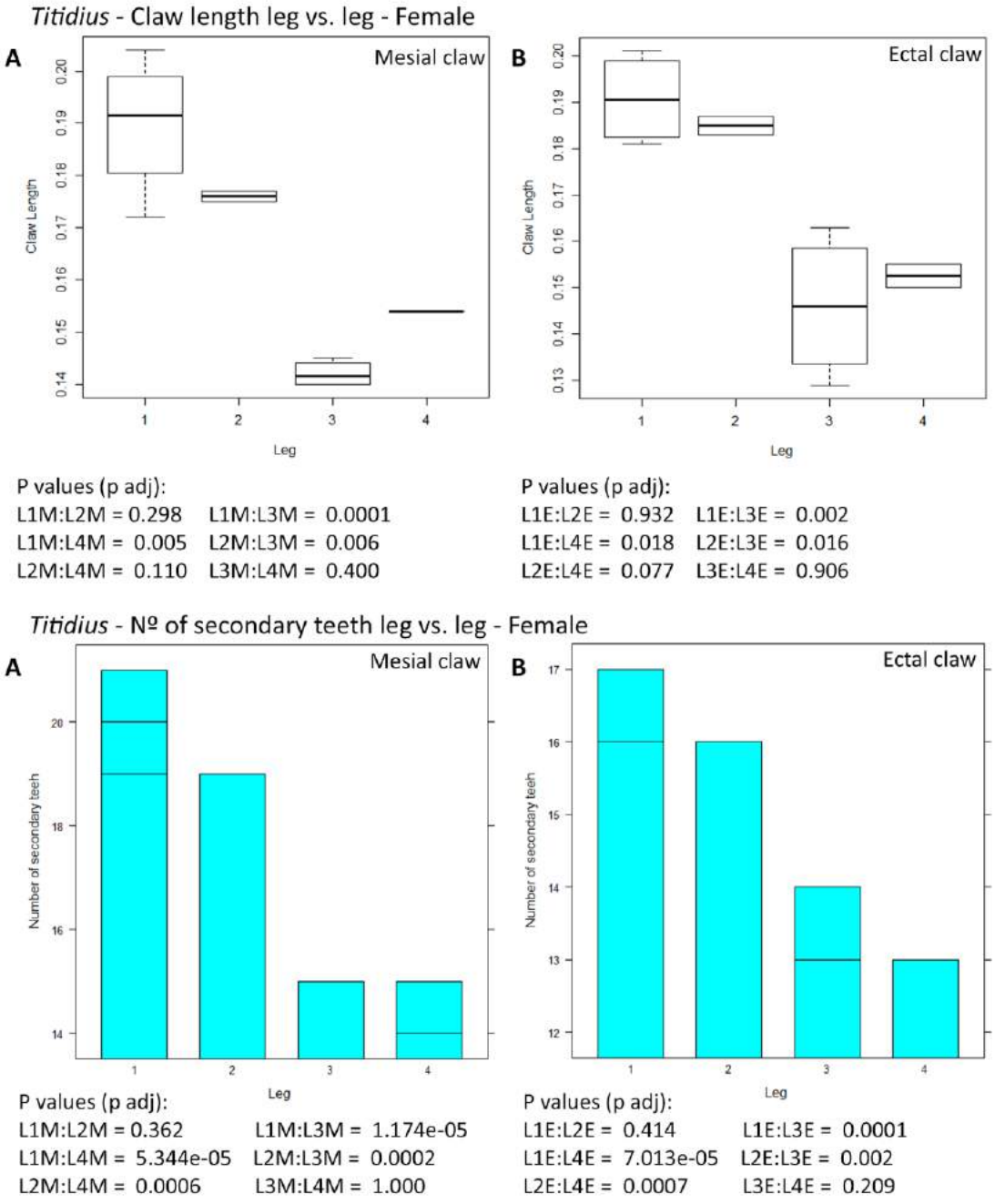
Graphic 16 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in males of *Stephanopis.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in males of *Stephanopis.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In males of *Stephanopis*. (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in males of *Stephanopis*.



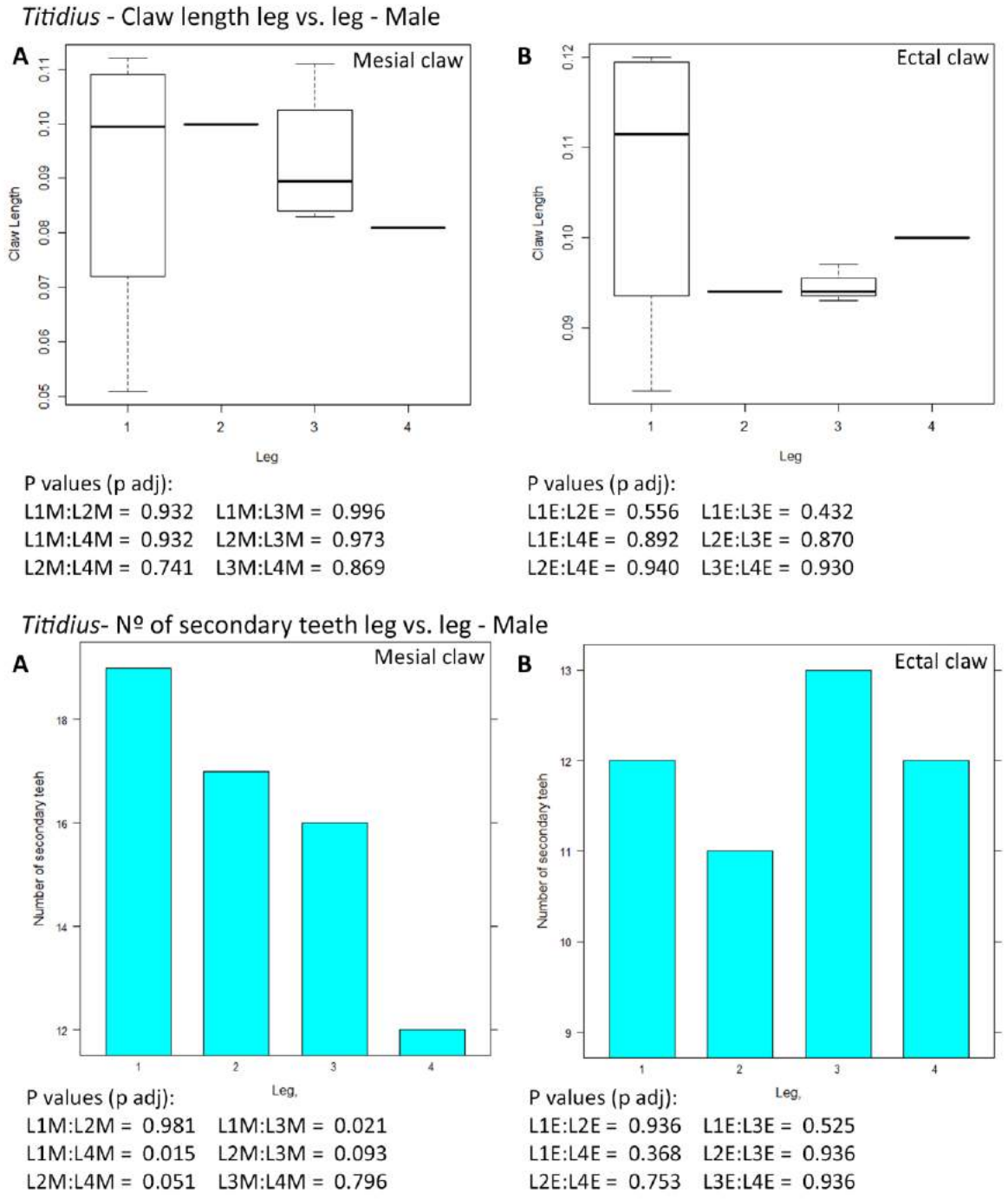
Graphic 17 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Strophius.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Strophius.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In males of *Strophius* (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Strophius*.



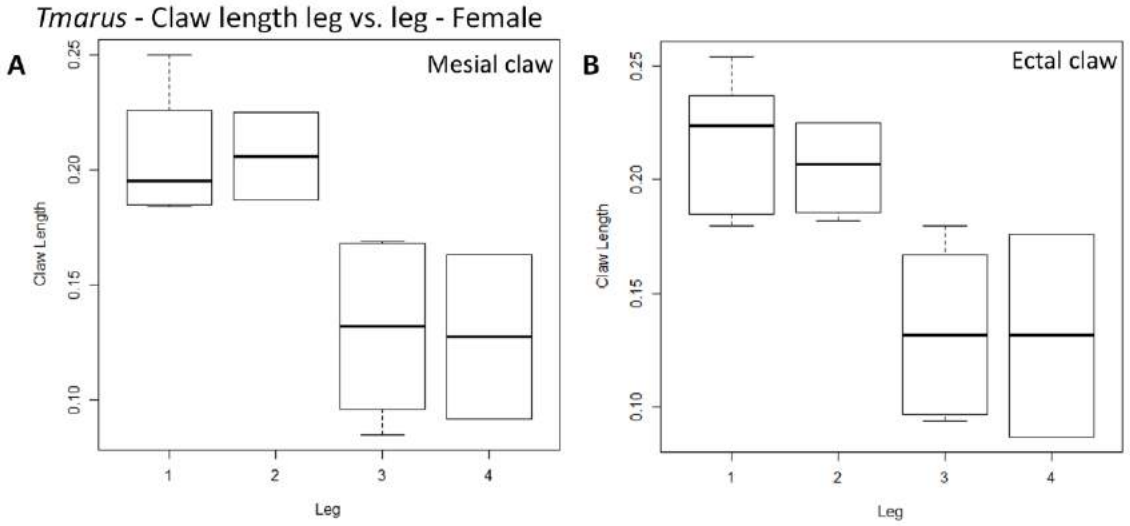
Graphic 18 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in males of *Strophius.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Strophius.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In males of *Strophius* (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in males of *Strophius*.



Graphic 19 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Titidius.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Titidius.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In females of *Titidius* (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Titidius*.

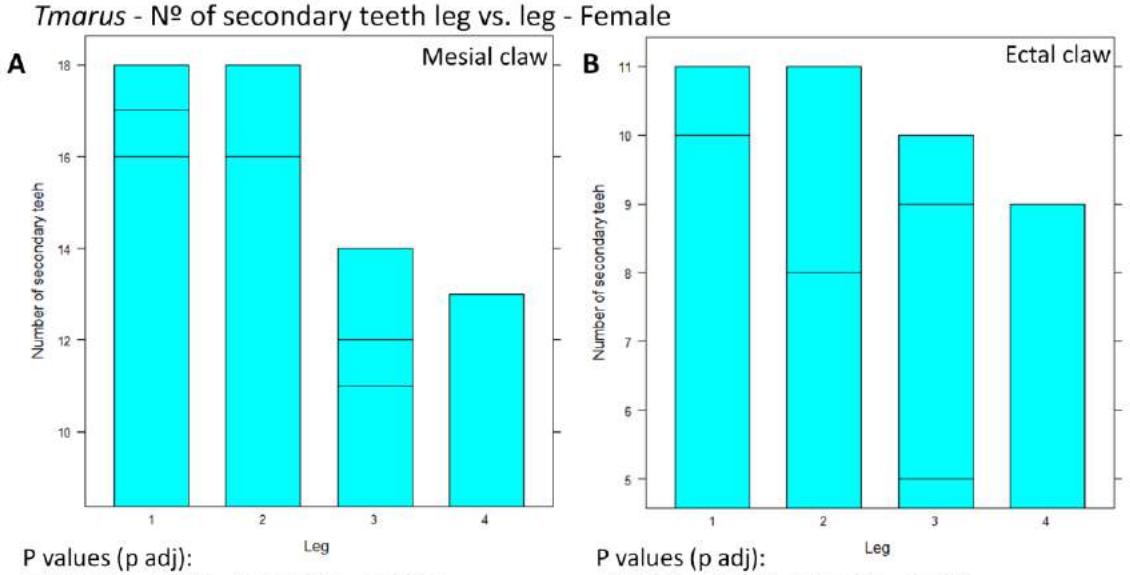


Graphic 20 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in males of *Titidius.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in males of *Titidius.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In males of *Titidius* (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in males of *Titidius*.



P values (p adj):
L1M:L2M = 0.999 L1M:L3M = 0.006
L1M:L4M = 0.011 L2M:L3M = 0.014
L2M:L4M = 0.021 L3M:L4M = 0.999

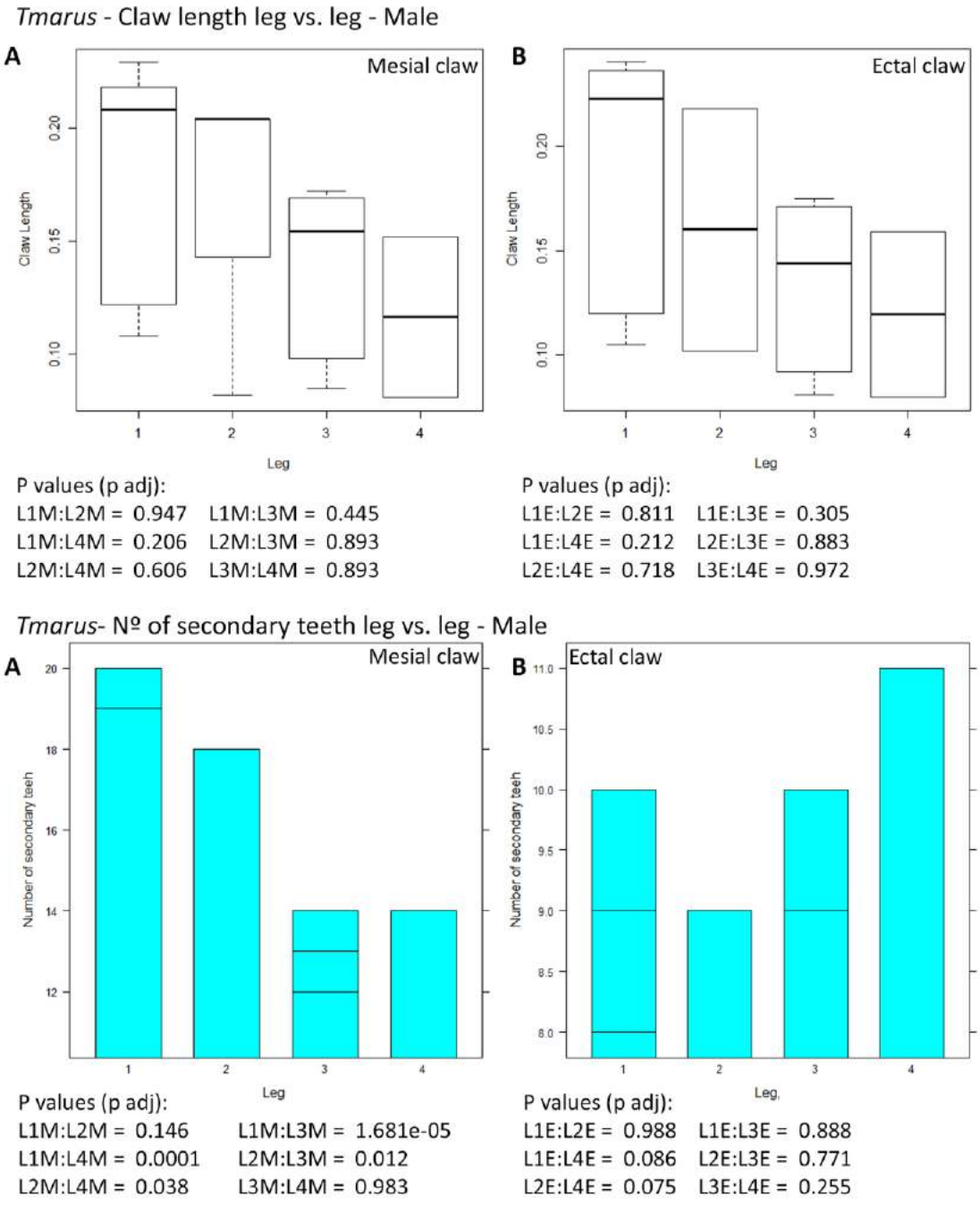
P values (p adj):
L1E:L2E = 0.957 L1E:L3E = 0.006
L1E:L4E = 0.012 L2E:L3E = 0.040
L2E:L4E = 0.057 L3E:L4E = 0.999



P values (p adj):
L1M:L2M = 0.947 L1M:L3M = 0.0001
L1M:L4M = 0.0009 L2M:L3M = 0.001
L2M:L4M = 0.0007 L3M:L4M = 0.983

P values (p adj):
L1E:L2E = 0.997 L1E:L3E = 0.485
L1E:L4E = 0.574 L2E:L3E = 0.685
L2E:L4E = 0.741 L3E:L4E = 1.000

Graphic 21 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in females of *Tmarus.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in females of *Tmarus.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In females of *Tmarus* (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in females of *Tmarus*.



Graphic 22 Upper graphics– (A) Boxplot comparing mesial claws' length between different legs in males of *Tmarus.* P-values of TukeyHSD pairwise tests are provided below the graphic. (B) Boxplot comparing ectal claws' length between legs in males of *Tmarus.* P-values of TukeyHSD pairwise tests are provided below the graphic. Lower graphics– (A) Bar plot comparing the number of secondary teeth in mesial claws between different legs. In males of *Tmarus* (B) Bar plot comparing the number of secondary teeth in ectal claws between different legs. in males of *Tmarus*.