Cladistic assessment and redescription of *Galodoxa torquata* Nagy (Hymenoptera, Bethylidae), a striking species with swallow tailed metasomal sternite

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Key words: Hymenoptera; Bethylidae; *Galodoxa*; Galodoxinae; Epyrinae; Sclerodermini.
Females of *Galodoxa torquata* Nagy, 1974, from the Oriental region, are promptly recognized by the deeply incised and bifurcate posterior margin of the fourth metasomal sternite. Because of this unusual character Nagy (1974) established a subfamily to accommodate it, but a superficial examination indicates that this species might be better placed in the tribe Sclerodermini. In order to test the hypothesis, it is redescribed, illustrated, and cladistically compared with data in literature of representative species of almost all genera of Sclerodermini and three outgroup species. A total of 72 characters extracted from literature are evaluated. The analyses were executed with equally weighted parsimony and implied weighting. Both unweighted and implied weighting results support the placement of *Galodoxa* into the tribe Sclerodermini. The monotypic subfamily Galodoxinae is therefore treated as new synonym of the subfamily Epyrinae and the genus *Galodoxa* Nagy, 1974 is transferred to the tribe Sclerodermini.

Introduction

The subfamily Galodoxinae was proposed by Nagy (1974) to include the very unusual species *Galodoxa torquata* Nagy, 1974, from the Philippines. This species was hitherto only known from the holotype. Nagy associated this taxon with the fossil genus *Protopristocera* Brues and the subfamily Pristocerinae, in spite of the fact that these groups are cladistically very distinct (Terayama, 1997).

While studying the collections of the National Museum of Natural History (Leiden), the Natural History Museum (London) and the Museum of Comparative Zoology (Cambridge, USA), we found three more specimens of *Galodoxa torquata* Nagy. However, our first impression of this species made us realise that *Galodoxa* might have more related to the subfamily Epyrinae, and particularly to the tribe Sclerodermini than to the Pristocerinae or *Protopristocera*.

The aim of this paper is to test the hypothesis that *Galodoxa torquata* belongs to the Sclerodermini, and to provide a redescription.

Materials and methods

The examined material was loaned from the National Museum of Natural History, Leiden NMNH - C. van Achterberg), the Museum of Comparative Zoology, Cambridge (MCZH - P. Perkins), and the Natural History Museum, London (BMNH - D. Notton).

Structural terms generally follow Evans (1964) and Azevedo (1999), but those related to the integument sculpture follow Harris (1979).

To assess the cladistic placement of this species we used the matrix provided by Lanes & Azevedo (2008) with 72 characters. The analyses were performed with PAUP 4.0 b10 of Swofford (1998) with the same settings (no limit to the number of trees kept in memory [maxtrees = 200 = auto autoinc = 200]; heuristic search with starting trees for branch swapping obtained by a random stepwise addition sequence, followed by TBR (tree bisection-reconnection) branch-swapping searching; 100 replicates carried out [hsearch start = stepwise addseq = random nreps =100 swap =tbr]; branches with null maximum length collapsed and duplicate trees deleted [condense collapse = maxbrlen deldupe = yes]). All character optimisations were performed using the default option (opt = acctran).

Analyses were executed with equally weighted parsimony and implied weighting with concave adjustment of Farris (1969) as modified by Goloboff (1993). In the implied weighting the fit (f) of each character (i) is calculated during the search with $f_i = (k+1)/(s_i + k + 1 - m_i)$, where k is the concavity parameter, s_i the effective number of steps of the character and m_i the minimum number of steps (Goloboff 1993). The total fit of the tree (F) is calculated with $F = \sum f_i$. The analyses with implied weighting were executed with values of k ranging from 0 to 5 [equivalent to the values from 1 to 6 in program Pee-Wee of Goloboff (1994; 1996)]. For the equal weights analyses we calculated the strict consensus tree and for the implied weights analyses we calculated the strict and the 50% majority rule consensus tree under all values of k (from 0 to 5).

Galodoxa Nagy, 1974

Galodoxa Nagy, 1974: 126-127; Gordh & Móczár, 1990: 171; Terayama, 2003a: 9 (list); Terayama, 2003b: 20 (key), 28 (list).

Diagnosis.— Clypeus with protruding median lobe. Notauli and parapsidal furrows present. Scutellar groove present. Upper and lower foveae of mesopleuron absent. Prosternum small. Fore wing with three closed cells. Metasomal sternite IV with pair of huge posterior expansions.

Description.— Clypeus with well projected trapezoidal median lobe. Antenna with 13 segments. Eye mostly placed on dorsal half of head. Occipital carina absent. Palpal formula 6:3. Pronotal disc with anterior corners subangulate. Notauli and parapsidal furrows present. Scutellum touching propodeal disc. Scutellar groove present. Propodeal disc without posterior carina; declivity without median carina. Mesopleuron with minute central pit, upper and lower foveae absent. Prosternum small. Coxae gibbous. Tibial spur formula 1:2:2. Tarsal formula 5:5:5. Fore wing fully developed, with three closed cells; submedian cell short and rectangular; prostigma and pterostigma contiguous. Metasomal sternite IV with pair of huge posterior expansions directed backward and downward.

Remarks.— Females of this genus are promptly recognized among Sclerodermini genera by the deeply emarginated posterior edge and strongly protruding lateral corners of metasomal sternite IV. This character is an autapomorphy within the family Bethylidae.

Galodoxa torquata Nagy, 1974
(figs 1-11)

Galodoxa torquata Nagy, 1974: 127-129 (description), 128 (figs 1-7); Gordh & Móczár, 1990: 171; Terayama, 2003a: 15 (list).

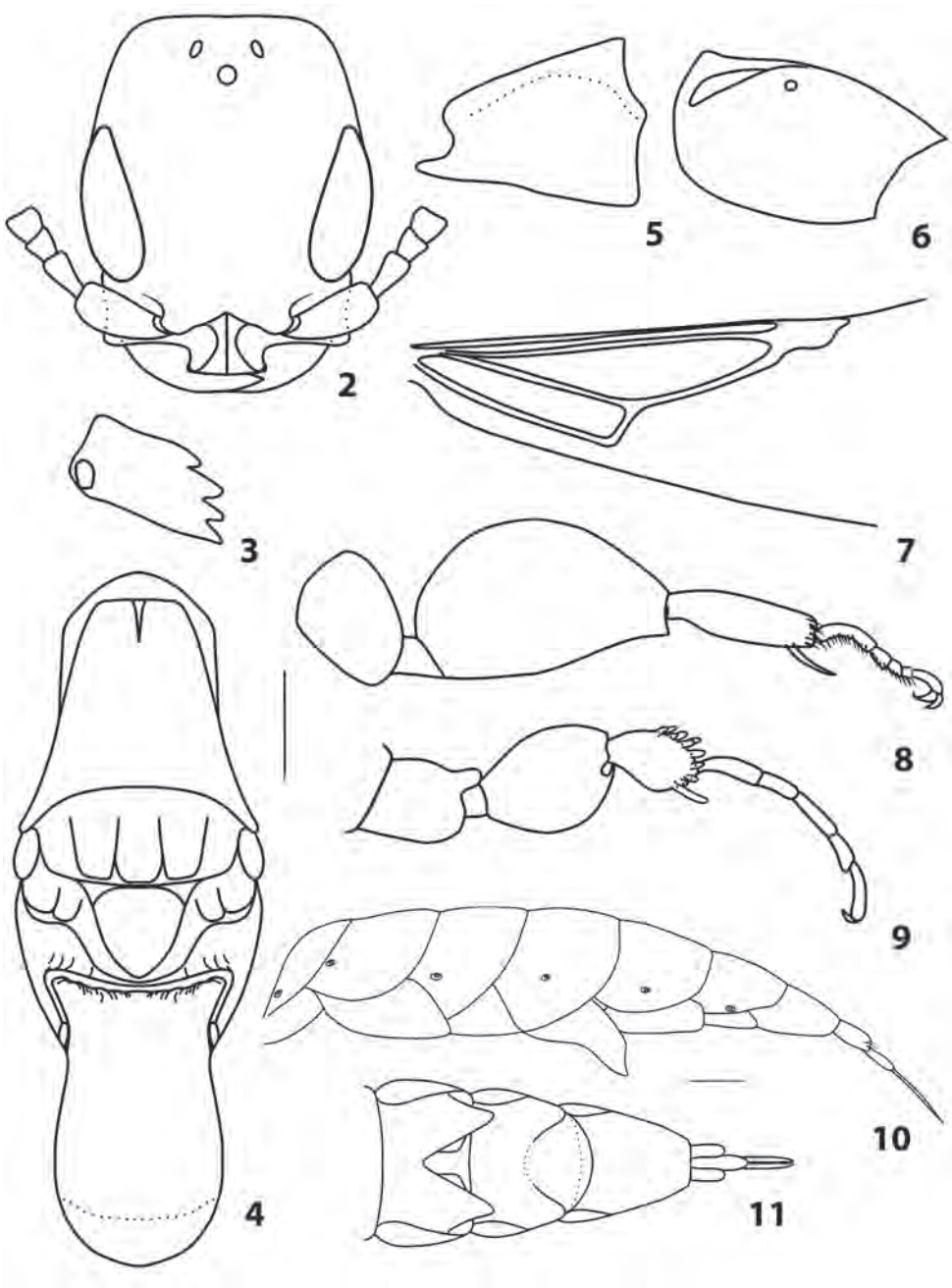
Material.— 1 ♀ **P[hilippines]**, Negro – Or[iental] Island, Dumaguete, 1500 f[ee]t [= 457 m], 3.vi.[19]49 (MCZH); 1 ♀ [**Indonesia**], Sulawesi, Utara, Dumoga-Bone N[ational] P[ark], 600 m, v.1985, Malaise trap, "below Edwards['camp]'', J. Martin col. (BMNH); 1 ♀ **Indonesia**, Halmahera, between Payahe & Gita Woda, Mal[aise] trap 4, c[irca] 20 m, 17.ii-17.iii.1995, C. v. Achterberg, R. de Vries & Y. Yasir, RMNH'95 (RMNH).

Diagnosis.— Mandible with four apical teeth. Pedicel longer than wide. Eye setose. Vertex straight. Notauli weak. Scutellar groove very shallow, apically not dilated. Propodeal disc without median and posterior carinae. Prosternum triangular. Fore femur strongly dilated. Fore tibia with a few distal spines; mid tibia with two lines of thick spines on posterior face; hind tibia with distal crown of thick setae and some distal spines. Claws simple.

Description, female (fig. 1).— Length of body 4.9-5.0 mm, length of fore wing 2.5-2.7 mm. Body castaneous to dark castaneous; coxae, trochanters and femora castaneous to dark castaneous; antenna, tibiae and tarsi light castaneous to castaneous; wings weakly to distinctly subhyaline; veins light castaneous to castaneous.

Head (fig. 2).— Mandible with four sharp apical teeth (fig. 3), overlapping each other about 50% of their length; with basal callus. Clypeus with a well projected trapezoidal median lobe, median longitudinal line elevated, carina straight in profile, base extending backward into frons between torulli for a short distance, triangularly shaped;

Figure 1. *Galodoxa torquata* Nagy, female, Indonesia (Halmahera), lateral aspect.



Figures 2-11. *Galodoxa torquata* Nagy. 2, head in dorsal view; 3, mandible in frontal view; 4, mesosoma in dorsal view; 5, pronotal disc in lateral view; 6, mesopleuron in lateral view; 7, fore wing in dorsal view; 8, internal face of fore leg in lateral view; 9, internal face of mid leg in lateral view; 10. metasoma in lateral view; 11, metasomal apex in ventral view. (bar = 250 μm; vertical bar for figs 2-9, horizontal for figs 10-11).

lateral lobe short and convex. Antenna moniliform, with 13 segments, scape with ventral side arched, flattened in cross section about 0.45 times as wide as long, pedicel longer than wide, flagellomeres about as long as wide, except for last one which is about 2.5 times as long as wide; pubescence short and appressed with many subappressed long setae standing out of regular pubescence. Eye oval, sparsely setose, mostly placed on dorsal half of head in lateral view. Frons weakly coriaceous, punctures sparse and small. Head 1.20-1.33 times as long as wide; width of frons 0.54-0.57 times head width and 0.90-0.98 times length of eye; ocello-ocular line 1.27-1.36 times width of ocellar triangle; ocellar triangle with obtuse frontal angle, distance from vertex crest 2.0-2.2 times diameter of anterior ocellus. Vertex straight in full dorsal view, corner rounded. Temple slightly bulging and diverging anteriorly in dorsal view. Vertex-ocular line 0.6 times length of eye. Gena mostly polished, completely separated from each other by a median carina. Hypostomal carina evenly arched. Palpal formula 6:3, segments with flattened cross section, widened distally, apices of segments with some setae nearly as long as segment.

Mesosoma (fig. 4).— Pronotal disc elongate, 2.2-2.3× as long as mesoscutum, weakly coriaceous, punctures sparse and small, anterior margin with weak transverse carina, anterior third of disc with longitudinal median linear depression, pronotal declivity concave in profile (fig. 5). Notauli very weak or nearly completely absent, connected to parapsidal furrows by an arched depression posteriorly. Parapsidal furrows very weak, absent anteriorly and nearly up to posterior margin of mesoscutum. Scutellum touching propodeal disc, scutellar groove very shallow and narrow, apically not dilated, obliquely arched backward. Propodeal disc areolate, median and posterior carinae absent, lateral carina very weak; spiracle elliptical, about 0.07 mm long, placed below lateral carina anteriorly; declivity weakly areolate, anterior transverse carina narrow, median carina absent; lateral surface of propodeum weakly areolate-coriaceous. Mesopleuron weakly coriaceous, central pit minute and comparatively dislocated upward, without any other foveae or pits (fig. 6). Propleuron rectangular in ventral view. Prosternum small, triangular with apex directed backward. Pleurosterna separated from each other by a narrow groove.

Wings (fig. 7).— Fore wing elongate, about 3.4 times as long as its maximum width; dorsal face setose, apical margin and distal half of posterior margin densely fringed; with three closed cells; costal cell very narrow and longitudinally folded, not visible in full dorsal view, costal vein narrower than subcostal vein; median cell semi-elliptical; submedian cell unusually rectangular, very short, about 0.5 times as long as median cell; prostigma triangular and pterostigma circular, not separated each other. Hind wing with costal vein short; dorsal face setose, apical margin and most of posterior margin fringed.

Legs (figs 7-8).— Coxae very shiny, especially fore coxa. Femora strongly dilated, especially fore femur, 1.5-1.7 times as long as wide. Fore and hind tibiae elongate, about 4.0 times as long as wide; fore tibia with some distal spines and with one apical spur; mid tibia wide, only 1.75-2.0 times as long as wide, with two lines of thick spines on posterior face and with two spurs; hind tibia with distal crown of thick setae and some distal spines, with two spurs. Tarsal formula 5:5:5; fore tarsus with fibula, segment I strongly arched, segments I and V much longer than wide, II-IV as long as wide, with some spines; mid tarsus with segment I arched, segment IV as long as wide, other much

longer than wide. Hind tarsus with all segments distinctly longer than wide, segment I-IV with fringe of thick setae on ventral face, about twice as long as diameter of segments. Claws simple and arched, apex sharp.

Metasoma (figs 9-10).— Not petiolate, constricted between sternites I and II. Tergites nearly smooth, posterior margin with few setae, laterally slightly more setose, first six tergites with pair of conspicuous lateral spiracles, near anterior margin in segment I-II and in middle in segments III-VI, posterior margin of segments I-V mostly straight medially, others distinctly convex. Posterior margin of sternites setose, otherwise almost not setose, smooth anteriorly to coriaceous posteriorly; posterior margin of segments III-IV straight, others convex; sternite IV with pair of huge posterior expansions directed backward and downward, 0.77-0.95 times as long as segment surface, posterior margin densely setose; surface of sternite V and anterior half of sternite VI covered by an aciculate membrane; surface of sternites V-VII slightly concave. Valvae III setose apically.

Variation.— The specimens of this series are very similar to the holotype. The holotype differs by its colour and the mandible teething. In this series the general colour is castaneous (specimen from Philippines) or dark castaneous (specimens from Indonesia), whereas the holotype is black. All three specimens here studied have the mandibles with four apical teeth, whereas the holotype has five-toothed mandibles.

Distribution.— Philippines and Indonesia. The description of *Galodoxa torquata* was based on only a single specimen, which was collected on southern Palawan island (Philippines) and 600 m above sea level. The three specimens examined here were collected on three other small islands, in altitude varying from 20 to 600 meters above sea level.

The female from the Philippines was collected in Dumaguete, which is located at the eastern side of Negro island. This city is distant from the type locality for about 600km. Both locations are separated from each other by the Sulu Sea.

One of the two females from Indonesia was collected in Dumoga-Bone National Park which lies toward the eastern extremity of the northern peninsula of the island Sulawesi. The other female was collected on the island Halmahera, which is the nearest island eastward of northern Sulawesi, disregarding some small islands. Both islands are separated from each other by the Moluccan Sea, which is about 260 km wide.

The distance between the two Indonesian sites and the two Philippinean sites is more than a thousand kilometers. This gap suggests that this species may have even a larger distribution.

Results

In the matrix, just 66 characters of *Galadoxa torquata* were codified, the characters 19, 27, 41, 48, 50 and 52 were considered inapplicable to this species, so they were assigned as "-". The characters included in the matrix are the following. **Head:** Subquadrangular (1:0) with ventral margin weakly convex in profile (2:1), temple convex (3:1) and vertex straight (4:0); maxillary palpus six-segmented (5:3); labial palpus three-segmented (6:2). Mandible with four teeth (7:0), upper margin continuous (8:0) and bristles long (9:1). Clypeus with median lobe longer than lateral lobes (10:0), median elevation thick (11:2), median carina present (12:1) and low (13:0), and basal margin surpassing posterior margin of antennal torullus (14:1). Antenna inserted laterally to the clypeus (15:1), with 13

segments (16:1) and antennal scape wide (17:0). Frontal groove absent (18:0). HE more than 0.38x LH (20:1). Eye localized in lateral of the head (gena not visible in dorsal view) (21:0), next to base of mandible (22:0) and prominent in relation to head surface (23:1). Ocelli present (24:1); centre of ocellar triangle not obliterated (25:1). Occipital carina absent (26:0). **Mesosoma**: Pronotal collar long (28:1). Pronotal disc with lateral margin weakly concave (29:0) and posterior margin straight (30:0). Prosternum narrow (31:0). Notauli present (33:1). Parapsidal furrow absent (34:1). Scutellum preeminent in relation to propodeum (35:0), with scutellar groove present (36:1) and narrow (37:0). Mesopleuron with subtegular groove present (38:1) and mesopleural elevation and prepectal carina absents (39:0 and 40:0, respectively). Metanotum absent (42:1). Propodeal disc with spiracles crescent-shaped (43:1) and lateral (44:0), anterior transverse carina present (45:1), anterior transverse carina inconspicuous (46:0), median discal carina absent (47:0), paramedian discal carina absent (49:0), lateral discal carina absent (51:0), lateral carina present (53:1) and straight (54:1), lateral foveolation open (55:0), sublateral carina absent (56:0), posterior transverse carina absent (57:0). Propodeal declivity with median carina absent (58:0) and lateral carina present (59:1). **Legs**: fore femur wide (32:1). **Wings**: forewing with marginal bristles elongate (60:1), costal vein present (61:1), median vein present (62:1), basal vein present (63:1), anal vein long (64:1), transverse median vein present (65:1), metacarpus vein absent (66:0), radial vein absent (67:0), submedian cell half of median cell (68:1); hindwing with three distal hamuli (69:1) adjacent (70:0) and jugal lobe partially fused to wing (71:1). **Metasoma**: acute tubercles of tergite IV and V absent (72:0).

Galodoxa always falls inside the Sclerodermini in all searches (see the different topologies in Lanes & Azevedo, 2008). Because of that *Galodoxa* is transferred from Galodoxinae to Epyrinae. Since Galodoxinae is a monotypic subfamily and consequently, *Galodoxa* is the type genus, this subfamily is considered as junior synonym of synonym of Epyrinae.

Galodoxa represented the most basal member of the tribe in the searches executed with equally weighted parsimony and implied weighting with $k = 0$, $k = 1$, $k = 2$ and $k = 3$, but it represented an intermediary member within the tribe in the searches executed with implied weighting with $k = 4$ and $k = 5$. In this case it forms a clade with *Alongatepyris* and *Thlastepyris*. As the goal is to test the hypothesis if *Galodoxa* belongs to the Sclerodermini no preferred cladogram was adopted.

Discussion

This genus has some peculiar features. The most evident one is the presence of the huge expansion of the metasomal sternite IV (figs 10, 11). This makes it promptly recognisable among bethylid genera, and consequently among the Sclerodermini genera. Nagy (1974) established a new subfamily because *Galodoxa* has this conspicuous and unusual condition. However the general feature of this genus resembles Sclerodermini as supported by the present results. Besides this, it has a wide antennal scape, the head with the occipital carina absent, the antennal insertion lateral to the clypeus in lateral view and the mesopleuron without lower fovea. All these conditions are shared with the other Sclerodermini genera.

However, *Galodoxa* has the clypeus with a well projecting median lobe (fig. 2) and the median clypeal carina is present. These two characters would address *Galodoxa* to

the Epyrini. The former character has been used to distinguish Epyrini from the other to Sclerodermini, although some species of Sclerodermini, including their species-type of the genus-type *Sclerodermus domesticus* Klug, also have the clypeus with well projecting median lobe when compared to others and have the clypeal median carina present. So, a clypeus with large median lobe seems to be a homoplastic character among the genera of Epyrinae and it is not useful for asserting the relationships of the genera of this subfamily.

The monophyly of Epyrini is ambiguous and there is no evidence that it constitutes one clade. Carpenter (1999) and Sorg (1988) were not able to find any synapomorphy. The most basal position of *Galodoxa* indicated by the results can be interpreted as a possible intermediary position of this genus between both tribes.

Another singular character is the presence of a membrane on the posterior margin of the apical sternites, which broadly overlaps the following sternite. Females of the Neotropical species of the *depressigaster* group of the genus *Epyris* all have such membranes similar to the condition in *Galodoxa*. In both cases the ventral surface of the metasomal apex is depressed or even slightly concave. The combination of both characters suggests that the females somehow hold the host before stinging it, for instance by pulling back the metasomal apex towards the host.

The mandible of *Galodoxa torquata* is unusually strong (fig. 3). It is very wide and thick compared to other species in the family. It is about half as wide as long and 0.3 times as thick as long. This bulky mandible can accommodate large muscles and suggests being a powerful tool to gnaw wood and explore galleries when searching for hosts.

The presence of a basal groove connecting the scutellar pits has been used to split Epyrini in two major groups, one with a groove such as *Anisepyris* Kieffer and *Rhabdepyris* Kieffer, and those without a groove such as *Trachepyris* and *Epyris* Westwood (see keys by Kieffer, 1905, Evans, 1964, Terayama, 2003). There is a huge and gradual variation in absolute or relative (to the pits) width, texture, length and depth of this groove. Such variation is also observed within the species of the same genus. This makes it a powerless character to be used in keys. In *Galodoxa* the scutellar groove is very shallow and sometimes even seems to be absent medially, depending on where the microscope light comes from, which emphasizes its weakness for keys.

The notauli and the parapsidal furrows are deeply impressed on the surface of the mesoscutum. Strangely enough, these pairs of furrows are connected posteriorly by a shallow arched linear depression. Because of that, the mesoscutum of some specimens seems to end in a joined triple U-shaped impression (uuu) in dorsal view (fig. 4). This feature was never recorded in any other Bethylidae.

The mesopleuron in *Galodoxa* is very simple when compared to that of other Epyrini (fig. 6), but it is very similar to those found in Sclerodermini species. In Epyrini the mesopleuron usually has four foveae (anterior, subtegular, lower and upper). The anterior fovea is placed close to the acetabular carina and is usually rounded or nearly so. The subtegular fovea is placed below the tegula; it is elongate and usually follows most of the dorsal margin of the mesopleuron. The lower fovea is generally the largest mesopleural fovea, it is also elongate and usually follows most of the ventral border of the mesopleuron. The upper fovea is placed in the center of the mesopleuron, above the lower one; it is usually elliptical or nearly so and contains the central pit. In addition there is an episternal suture which follows the posterior margin of the mesopleuron. In *Galodoxa* the

anterior, the lower and the upper foveae, as well as the episternal suture are absent. The subtegular fovea is confined to the anterior region of the dorsal margin of the mesopleuron, exactly below the tegula. The central pit is small and dislocated in upward direction. The simplicity of the mesopleural sculpture connects *Galodoxa* to the Sclerodermini, where most of genera have a mesopleuron without such foveae or sutures.

The fore wing venation is also unusual (fig. 7). The submedian cell is usually about as long as median cell in Bethylidae, except for Bethylinae species where it is about 70-80% of the length of the median cell. In *Galodoxa* the submedian cell is no more than 0.5 times as long as the median cell, as in a few other genera of Bethylidae such as the genera *Thlastepyris* Evans and *Alongatepyris* Azevedo of the Sclerodermini. The presence of this character groups these three genera when the searches were executed with implied weighting with $k = 4$ and $k = 5$. The apex of this cell is blunt as in *Thlastepyris* (see fig. 12 in Evans, 1973), whereas it is rounded in *Alongatepyris* (see fig. 1 in Azevedo, 1992).

Another unusual feature of the fore wings is the contrast between the tubular and well pigmented venation on the basal half of the wing and the complete absence of a radial vein or any other vein on the apical half. Generally, genera without radial vein have at least some veins, or parts of them spectral or weakly pigmented, such as in *Cephalonomia* Westwood and *Sclerodermus* Latreille (see figs 10 and 12 in Evans 1978). This contrast can also be observed in few other genera of Epyrini with short radial vein such as *Laelius* Ashmead and *Disepyris* Kieffer (fig. 8 in Evans, 1978). In these genera the radial vein ends abruptly at short distance of the stigma. *Trachepyris* Kieffer also has a short radial vein, but in this case it is contrastingly thinner than the veins on the basal half of the wings.

Several genera of Sclerodermini have no costal vein, and because of that the costal cell is opened. The costal cell in *Galodoxa* is closed and the costal vein is present, although distinctly narrower than the other veins (fig. 7). This homoplastic character is shared with *Alongatepyris*, *Bethylopsis* Fouts, *Allobethylus* Kieffer and with a few species of *Glenosema* Kieffer, in such a way that it is not useful to define clades in the Sclerodermini.

Bethylidae usually have the fore femur swollen (Azevedo, 2006). Among chrysidoid families Sclerogibbidae stand out by having females with the fore femur strongly swollen. In the females of this family the fore femur is raptorial and much larger than the mid and hind femora (Olmi, 2004). *Galodoxa* seems to represent an extreme of this feature within bethylids, being only about 1.6 times as long as wide (fig. 8). This is comparable to those of some species of Sclerogibbidae and certainly one of the most strongly swollen fore femora in Bethylidae. The dilated fore femur in females of Bethylidae has been associated with fossorial behavior, but Vargas & Terayama (2006) restricted this association only to apterous females. *Galodoxa* has the other femora and all coxae unusually dilated (figs 8, 9), so that the legs are very musculate and suitable for crawling inside the galleries to search for host in the wood.

The mid tibial spines are placed on the anterior face of the tibia in most of the bethylid species. Curiously the mid tibial spines in *Galodoxa* are placed on the outer face rather than on the anterior face (fig. 9). It is important to point out that the anterior face of the mid tibia is laterad and the outer face is posterad. These spines are disposed in two rows rather than evenly spread on the surface. In addition, they are flattened in transverse section rather than cylindrical as usual in Bethylidae.

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