
Systematics of the sycoecine fig wasps (Agaonidae, Chalcidoidea, Hymenoptera), II (*Sycoecus*)

S. van Noort

Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa

Present address: Department of Entomology, South African Museum, P.O. Box 61, Cape Town, 8000, South Africa

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ABSTRACT

Sycoecus Waterston, an African genus of fig wasps, is revised. Members of this genus are all associated with the *Ficus* (Moraceae) subsection *Cyathistipulae* of section *Galoglychia*. These fig trees are pollinated by agaonines of the genus *Agaon* Dalman. Nine new species are described in this previously monospecific genus: *Sycoecus oculabulbus* (Cameroun, ex *Ficus cyathistipulae pringsheimiana* (Braun & Schum.)), *S. taylori* (ex, *Ficus spec.*), *S. ivoryensis* (Ivory Coast, ex *F. scott-elliottii* Mildbr. & Burr.), *S. lamtoensis* (Ivory Coast, ex *F. sagittifolia* Mildbr. & Burr.), *S. crinitus* (ex *F. lyrata* Warb.), *S. wiebesi* (ex *F. cyathistipuloides* De Wild and *F. subsagittifolia* Berg), *S. medleri* (ex *F. 'winkleri'*), *S. bergi* (ex *F. tessellata* Warb.), and *S. nyassossoensis* (ex *Ficus spec.*). The male of *S. thaumastocnema* Waterston is described for the first time. A key is provided to separate the species in both sexes.

INTRODUCTION

Sycoecus Waterston is the only African sycoecine genus to maintain its original delimitations in the current revision and is probably the most distinctive genus found on the continent. Ten species are now known in this genus, nine of which are described here for the first time. The species are all associated with *Ficus* species belonging to the subsection *Cyathistipulae*, section *Galoglychia*, which are only pollinated by agaonines of the genus *Agaon* Dalman. As a result, *Sycoecus* is one of two African sycoecine genera (the other is *Seres* Waterston) to be restricted to a single *Ficus* subsection and to be associated with a single agaonine genus. In addition the association is tighter, since *Sycoecus* is the only sycoecine genus to be associated with subsection *Cyathistipulae*, whereas the

host subsection of *Seres* (subsection *Caulocarphae*) is also host to species of two other sycoecine genera.

Morphological terminology, definitions and abbreviations are as defined in van Noort (1993). All measurements are in millimeters. The following acronyms are used for institutions and collections housing *Sycoecus* specimens:

NHML – The Natural History Museum, London
RMNH – Rijksmuseum van Natuurlijke Historie, Leiden
SAMC – South African Museum, Cape Town
SANC – National Collection of Insects, Pretoria
SGCC – Collection of Dr. S.G. Compton, Leeds

Sycoecus Waterston

Sycoecus Waterston 1914, 253.

Type species: *Sycoecus thaumastocnema* Waterston 1914, by monotypy.

FEMALE. Head elongate, dorso-ventrally flattened; smooth, no sculpture; clypeus narrow, produced at the epistomal margin, with a medial concavity of varying depth; toruli in close apposition; malar sulcus present, posteriorly as a fovea, but fading out or very indistinct towards the oral fossa. Compound eyes situated posteriorly on face, in proximation with the vertex. Vertex excavated laterally, excavation extending through the temples to the posterior eye margin. Lateral ocelli usually situated on the inside of the axial lip, and thus hidden or partially hidden from dorsal view, except in some species where the excavation is weak. Medially the vertex has a raised prominence between the lateral ocelli, on the posterior edge of which runs the occipital carina. This carina encircles the top half of the foramen magnum, which is situated posteriorly in proximation with the vertex, such that the occiput is absent. Strong setae are present on the vertex. Ventral tentorial pits separated, situated about half way between the oral fossa and the foramen magnum. Hypostoma usually reduced, sometimes complete. Cardo reduced or absent, posterior portion of stipes overlaps hypostomal area. Four maxillary palp segments, proximal and third segments subequal, second slightly shorter and apical segment ca. twice as long as each of the first three; two labial palp segments, basal segment half to two-thirds as long as the distal. Mandible with two apical teeth, two or three ventral teeth, proximally the ventral edge is a sharp ridge; blunt lobe in molar region for muscle attachment; two glands, inner reduced and small. Dorsal tentorial pits situated on clypeal sutures, closer to the epistomal margin than to the toruli. Antenna eleven segmented, formula 1124(3), pedicel short, first anellus reduced in comparison to the second; first funicle segment expanded on the inner margin, lateral margins convex, about as long as wide, remaining funicle segments longer than wide; first three funicle segments dorso-ventrally flattened, fourth segment subcylindrical, club segments cylindrical, tapering towards the apex. Multiporous plate sensilla

(MPS) placoid, thin and elongate, present in alternating rows, absent or reduced on the ventral surface.

Thorax dorso-ventrally compressed; smooth, without sculpture; pronotum elongate, compressed laterally, with a carina on the dorso-anterior margin, two slight lateral depressions present for almost the length of the pronotum (inner margin of which is visible as a carina in slide mounts); the sides of the pronotum below the lateral depressions with broad concave excavations; mesonotum subtriangular, parapsidal sulci complete, straight; propodeal sulci well defined with a pronounced ridge defining the axial edge, spiracles anteriorly situated in the sulci. A few strong setae present. Propleura with pronounced excavations. General form of legs typical for sycoecines; fore femur stout, elongate, subcylindrical; adaxial face of fore tibia with two rows of stout teeth, inner row with fewer, stronger teeth. Fore tibial spur highly modified and expanded to form a plate of many teeth or spines on the antiaxial surface, axial surface smooth, articulation of spur more proximally situated on tibia than normal for the subfamily. Ventral tooth, situated next to the spur insertion, absent. Hind coxa usually with a medial posterior plica on axial face. Axial third of forewing glabrous, rest covered in microsetae; fringe present. Marginal vein thickened; postmarginal vein subequal to longer than the stigmal vein.

Gaster with five to seven evenly spaced slit-like incisions on the posterior edge of the tergites, otherwise edge smooth. Eighth urotergite spiracle normal, dorso-laterally situated. A setal patch of variable density situated posterior to the spiracle. Ovipositor valves variable in length.

MALE. Head slightly elongate, narrowing anteriorly in dorsal view, not very compressed in lateral view, height about two-fifths of length; clypeus subtriangular in area, epistomal margin broader than in the females. Toruli always separated, situated below the eyes, closer to the epistomal margin than to the vertex. Antennal formula 1124(3), second anellus almost 3X the length of the first, and half the length of the funicle segments. MPS usually present as a single row, sometimes as two rows. Dorsal tentorial pits present on the lateral clypeal sutures closer to the epistomal margin than to the toruli. Malar sulcus present for the first quarter to two-thirds of the cheek length. Lateral ocelli usually situated in axial end of a shallow excavation on the vertex. Medial prominence present on the vertex between the lateral ocelli, with the occipital carina situated along the posterior edge, dorsal to the foramen magnum. Carina approximately straight. Eight to ten strong setae present on the vertex. Ventral tentorial pits separated, situated ca. half way between the foramen magnum and the oral fossa. Hypostoma present, hidden by stipes medially. Four maxillary palp segments, two labial palp segments, ratios much as in the females. Mandible with a single ventral tooth, short apical tooth and a shorter dorsal subapical tooth, two glands, subapical gland smaller.

Thorax. Pronotum subquadrate; mesonotum subtriangular, parapsidal sulci straight or slightly curved anteriorly. Axillae larger than in the females. Propodeal sulci present in varying degrees, spiracles anteriorly situated. Strong setae present

on the thorax, positions much as in the females. No excavations on the propleura. Two strong dorso-apical teeth on the fore tibia, dorsal tooth twice as large; spur slightly modified and expanded, more proximally situated on the tibia as in the females; no ventral tooth. Wings pilose, axial third of fore wings bare, axial fifth to quarter of hindwings bare, rest of wings covered with microsetae, medial and anal setal tracts present, fringe present. Marginal vein thickened.

Gaster, posterior edge of tergites uniformly straight, with small setae along the edge. Aedeagus large.

Comments. *Sycoecus* is probably the most ancestral sycoecine genus (van Noort & Compton, in prep.) with sexual dimorphism the least pronounced of any of the genera. *Sycoecus* also has the primitive chalcidoid complement of four maxillary palp segments and pronounced propodeal plicae. Nonetheless the monophyly of this genus is strongly supported by a number of autapomorphies in the females. These include the modification of the fore tibial spur into a plate of many fine teeth; the axial expansion of the first funicle segment; excavation of the propleura and the presence of lateral pronotal depressions.

Most of the above autapomorphies have evolved as adaptations to facilitate ostiolar entrance by the female. The lateral depressions on the pronotum appear to have evolved to accommodate the flagellum, so as to prevent damage to the antennae and the MPS when they are folded back on entering the ostiole, much as the antennal scrobe protects the scape and pedicel or even the flagellum in genera where this is short. The *Sycoecus* flagellum is relatively the longest amongst the sycoecine genera and this may explain why these pronotal depressions are only present in this genus. The dorso-ventral flattening of the flagellum in combination with a lack of MPS on the ventral surface (which becomes the exposed dorsal surface when the antennae are folded back), must also facilitate the preservation of the antennae while the wasp is entering the ostiole. This either indicates that the antennae and MPS are necessary for the oviposition process or that *Sycoecus* also leaves the fig after oviposition and enters further figs, as do some of the *Philocaenus* species. If this were so, the preservation of the antennae would be essential for the olfactory location of other figs that were ready for pollination.

The propleural excavations appear to be adaptations to accommodate the fore tibia and tarsi when the female negotiates the ostiole (the femur would still be held in apposition with the side of the pronotum as in the other sycoecine genera). The tibial plate would then close off the excavation, such that only the tibial teeth and teeth on the tibial plate project from the flush surface. This presumably facilitates the streamlining required for ostiolar penetration.

KEY TO THE SPECIES OF *SYCOECUS*

FEMALES

1. Tibial plate distinctly (more than 1.3X) longer than total fore tibial length (figs. 19, 21 & 38); epistomal margin indentation no deeper than the projection of the margin (figs. 11, 22, 29 & 36) ... 2

- Tibial plate subequal (less than 1.13X as long) to fore tibial length (figs. 9, 10 & 16); epistomal margin indentation deeper than the projection of the margin (figs. 1, 4, 6 & 13) 7
- 2. Mandible with two ventral teeth (figs. 5, 7, 18, 20 & 26) 3
- Mandible with three ventral teeth (figs. 15 & 35) 6
- 3. Tibial plate more than twice as long as total fore tibial length 4
- Tibial plate less than twice as long as fore tibia 5
- 4. Cheek 1.6X longer than eye length (fig. 20); tibial plate 2.6X longer than fore tibia, ex *F. lyrata* ..
..... *S. crinitus*
- Cheek at least twice as long as eye (fig. 37); tibial plate 2.3X longer than fore tibia, ex *F. cyathistipuloides* and *F. subsagittifolia* *S. wiebesi*
- 5. Tibial plate 1.3X as long as fore tibia; cheek 1.2X as long as eye, ex *F. sagittifolia* .. *S. lamtoensis*
- Tibial plate 1.8X as long as fore tibia; cheek 1.6X as long as eye, ex *F. scott-elliotti* .. *S. ivoryensis*
- 6. Epistomal margin indentation shallower than its width (fig. 36); cheek 1.76X longer than eye, ex *Ficus spec.* *S. nyassosoensis*
- Epistomal margin indentation deeper than its width, cheek 1.12X longer than eye, ex *F. c. cyathistipula* *S. thaumastocnema*
- 7. Mandible with three ventral teeth; cheek length 1.34X longer than eye length, ex *F. tesselata*
..... *S. bergi*
- Mandible with two ventral teeth; cheek length either 1.46X, subequal or shorter than eye length 8
- 8. Cheek length 1.46X longer than eye, ex *Ficus spec.* *S. medleri*
- Cheek length shorter or subequal to eye length 9
- 9. Cheek length shorter than eye length (fig. 7); indentation in epistomal margin as broad as the width of both toruli (fig. 1), ex *F. cyathistipula pringsheimiana* *S. oculabulbus*
- Cheek subequal to eye length; indentation narrower, width equivalent to the width of one torulus (fig. 6), ex *Ficus spec.* *S. taylori*

MALES*

- 1. Bilobed epistomal margin, with the medial concavity equivalent in size to each lateral convexity (fig. 2); vertex, mesoscutum and gaster dark brown, rest testaceous, ex *F. c. pringsheimiana*
..... *S. oculabulbus*
- Epistomal margin almost straight, with a medial concavity absent or minute; completely testaceous 2
- 2. Epistomal margin almost straight with no medial concavity (fig. 30), ex *F. cyathistipuloides*
..... *S. wiebesi*
- Epistomal margin with a medial impression which may be very broad and shallow (figs. 12, 14 & 27) 3
- 3. Epistomal margin convex with a broad and very shallow medial concavity (fig. 27); toruli separated by a third of torulus width (fig. 27), ex *F. lyrata* *S. crinitus*
- Epistomal margin with a distinct, small, medial impression, ca. as deep as wide (figs. 12 & 14); toruli separated by more than half the width of a torulus 4
- 4. Head 1.16X longer than wide, eye length 1.20X longer than the cheek; toruli separated by less than the width of a torulus, ex *Ficus spec.* *S. nyassosoensis*
- Head less than 1.09X longer than wide, eye more than 1.30X longer than the cheek; toruli separated by the width of a torulus 5
- 5. Eye length 1.47X longer than the cheek, ex *F. c. cyathistipula* *S. thamastocnema*
- Eye length 1.31X longer than the cheek 6
- 6. SL 2.4X longer than TE; head slightly elongate L:W = 1.08 (fig. 12), ex *F. sagittifolia*
..... *S. lamtoensis*
- SL 2.7X longer than TE; head ca. square L:W = 1.02 (fig. 14), ex *F. tesselata* *S. bergi*

*The males of *S. taylori*, *S. ivoryensis* and *S. medleri* are unknown.

Sycoecus oculabulbus spec. nov.

(figs. 1-3 & 7-10)

Etymology: Ocula (latin) = eye, bulbus (latin) = bulb, referring to the large bulbous eyes.

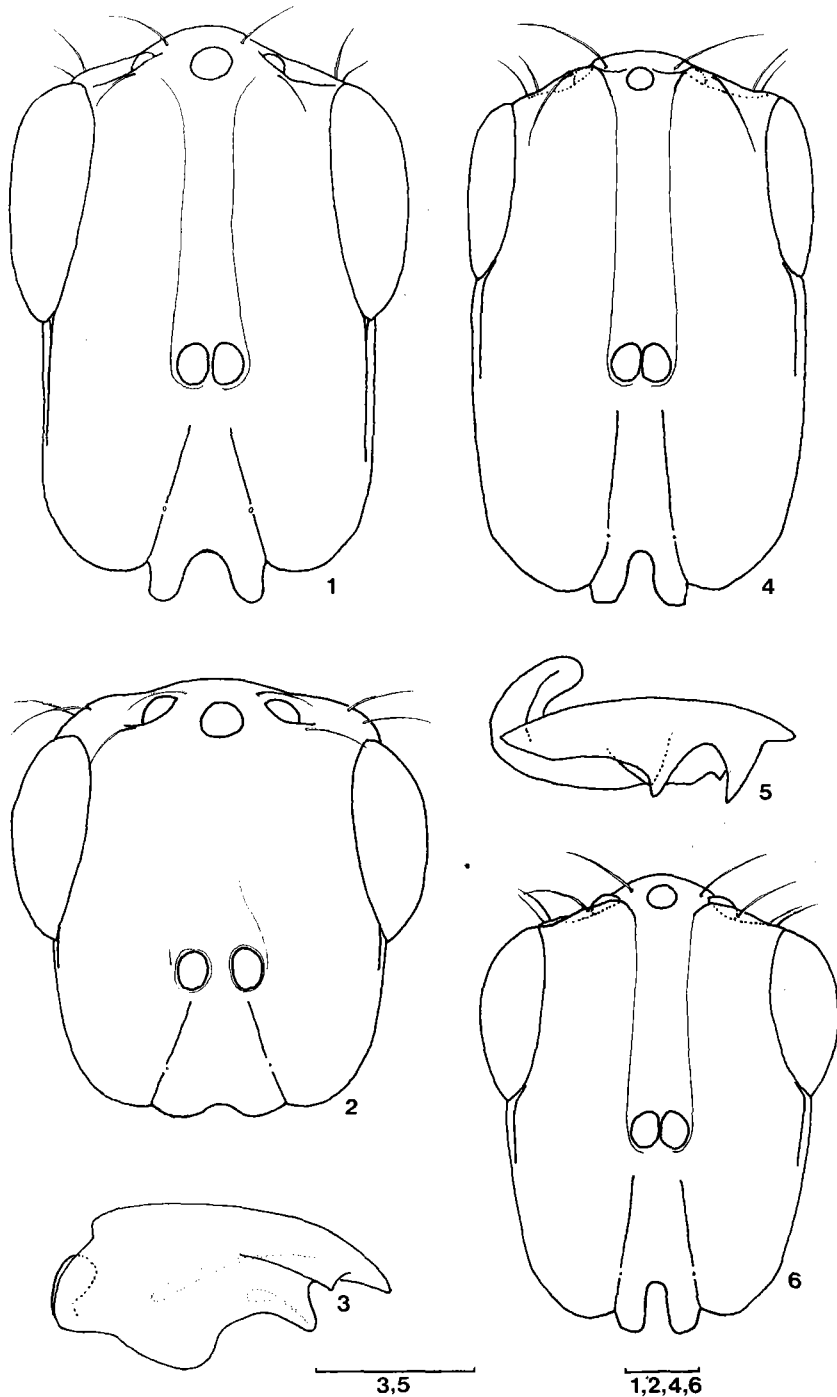
Type material: Holotype ♀, allotype ♂, (slide mounted): Cameroun, South West Province, Bambili, 28 December 1981, leg. S.G. Compton & R.G.E. Baker, C1013, ex *F. cyasthistipula pringsheimiana* (Braun & Schum.). Paratypes, 3 ♀♀, (slide mounted), 10 ♀♀, 3 ♂♂, (card mounted): same data as holotype. Holotype, allotype and some paratypes in SAMC. Other paratypes in SGCC, RMNH, NHML and SANC.

FEMALE. Metallic black, legs (excluding hind coxae), and antennae testaceous. Total length with head in orthognathous position excluding ovipositor 2.7 mm.

Head (figs. 1 & 7) elongate, parallel sided ($l = 0.77$, $w = 0.54$, $h = 0.23$), wedge shaped in lateral view, convex dorsally, flat ventrally. Eye elongate ($l = 0.32$, $w = 0.18$, $h = 0.32$), 0.41X as long as head. Cheek length 1.2X longer than eye. Malar sulcus present for most of cheek, fades out for last quarter, curves slightly dorsad. Lateral ocelli large, completely visible in dorsal view; lateral excavations on vertex very shallow; medial ocellus situated in posterior end of scrobe. Occipital carina on the medial prominence broad and open, not extending in a tight U around the foramen magnum. Excavation around foramen magnum broad and shallow. POL = 0.14. OOL = 0.07. Toruli slightly separated, situated below the eyes; TE 0.7X as long as scrobe length (SL = 0.41). Clypeus trapezoid in area. Epistomal margin convex with medial indentation extending deeper than paraclypeal margins, three-tenths of head width. Hypostoma complete. Mandible with two ventral teeth close together, situated nearer the apex, proximally the ventral edge is a plain ridge (fig. 7). Antennal flagellum (fig. 8) ($l = 0.94$) longer than head. Scape 6.8X longer than wide ($l = 0.31$). Pedicel a quarter of scape length. Multi-porous plate sensilla present as 3 to 4 alternating rows on funicle and first club segments, as two rows on penultimate and as one row on ultimate club segments (fig. 8). MPS absent on ventral surface of first two funicle segments. Funicle segments subequal in length.

Thorax. Pronotum elongate ($l = 0.43$, $w = 0.39$), trapezoid. Propodeum $l = 0.26$, $w = 0.43$. Mesoscutum $l = 0.36$, $w = 0.50$. Scutellum, including axillae ($l = 0.43$, $w = 0.42$). Fore femur 4.2X longer than wide ($l = 0.61$), 1.5X longer than fore coxa ($C = 0.40$, TR = 0.13, TI = 0.22, TA = 0.35). Fore tibial plate same length as tibia, with few coarse teeth. Inner row of teeth on adaxial face of fore tibia with nine-eleven teeth, outer with six teeth (figs. 9 & 10). Hind coxal plica absent. Fore wing ($l = 2.39$, $w = 1.04$) very pilose, maximum fringe length = 0.08, anal and medial setal tracts present. Postmarginal vein longer than stigmal (SM = 0.79, M = 0.34, PM = 0.28, S = 0.25). Marginal vein 6.8X longer than wide. Hind wing 4X longer than wide ($l = 1.68$).

Gaster. Few setae present on hypopygium. Eighth urotergite spiracle $l = 0.037$. Ovipositor 6.3X longer than ovipositor valve, $l = 0.20$.



Figs. 1-3. *Sycoecus oculabulbus* spec. nov.: 1, female head, dorsal view; 2, male head, ventral view; 3, male mandible, ventral view. Figs. 4-5. *Sycoecus medleri* spec. nov.: 4, female head, dorsal view; 5, female mandible, ventral view. Fig. 6. *Sycoecus taylori* spec. nov.: 6, female head, dorsal view. Scale bars = 0.1 mm.

MALE. Testaceous, posterior half of head, flagella, eyes, mesoscutum, axilla and gaster dark brown. Total length with head in orthognathous position 2.34 mm.

Head (fig. 2) elongate ($l = 0.59$, $w = 0.55$), height normal ($h = 0.25$). Eye elongate ($l = 0.27$, $w = 0.16$), protrudes laterally ($h = 0.10$), $0.46X$ as long as the head. Cheek length $0.67X$ eye length. Malar sulcus present for first two-thirds of cheek. Lateral ocelli visible in dorsal view situated in very shallow depression. $POL = 0.12$, $OOL = 0.08$. Toruli separated by ca. half of torulus width, $TE = 0.50X$ as long as scrobe length, $TE = 0.17$, $SL = 0.34$. Width of clypeal margin $0.31X$ head width. Mandible as in fig. 3. Antennal flagellum $5.6X$ pedicel length. Scape $4.5X$ longer than wide ($l = 0.27$). Pedicel $0.33X$ scape length. MPS present as two alternating rows with a total of 9, 9, 9 & 10 (starting at the proximal segment) sensilla on the funicle segments respectively and a single row of 7, 7 & 4 sensilla on the club segments respectively.

Thorax. Parapsidal sulci curved anteriorly. Propodeal plical furrows complete. Fore femur $3.8X$ longer than wide, $l = 0.53$. Fore tibia $1.5X$ longer than tarsus ($C = 0.38$, $TR = 0.12$, $TI = 0.37$, $TA = 0.24$). Fore wing $2.4X$ longer than wide, $l = 2.25$. Postmarginal vein same length as stigmal ($SM = 0.73$, $M = 0.32$, $S = 0.26$, $PM = 0.26$). Marginal vein $8X$ longer than wide. Hind wing $4.3X$ longer than wide, $l = 1.56$.

Gaster. Eighth urotergite spiracle small and round. Aedeagus large ($l = 0.75$). Four teeth on aedeagus claspers.

Comments. *S. oculabulbus* is most similar to *S. taylori*, but can be separated by the longer eye relative to cheek length and the wider and broader medial indentation in the epistomal margin.

Sycoecus taylori spec. nov.

(fig. 6)

Etymology: Named after the collector of the holotype.

Type material: Holotype ♀ (slide mounted): Uganda, 1939, leg. T.H.C. Taylor, T850. Paratypes, 1♀ (slide mounted), 4♀♀ (card mounted): same data as holotype. Holotype and some paratypes in SAMC. Other paratypes in SGCC, RMNH, NHML and SANC.

FEMALE. Faded, due to alcohol storage, probably metallic black. Total length with head in orthognathous position excluding ovipositor 2.0 mm.

Head (fig. 6) elongate, parallel sided ($l = 0.63$, $w = 0.49$, $h = 0.19$), wedge shaped in lateral view, not as dorso-ventrally compressed as previous species, convex dorsally, flat ventrally. Eye oval ($l = 0.24$, $w = 0.15$, $h = 0.08$), $0.38X$ as long as head. Cheek $l = 0.25$ slightly longer than eye. Malar sulcus definitely present for the first half and possibly the whole of the cheek length (difficult to determine due to poor preservation). Lateral ocelli visible in dorsal view, excavations on vertex very shallow, medial ocellus situated in posterior end of scrobe. Medial prominence on vertex with strong occipital carina, open as in *S. oculabulbus* but not as