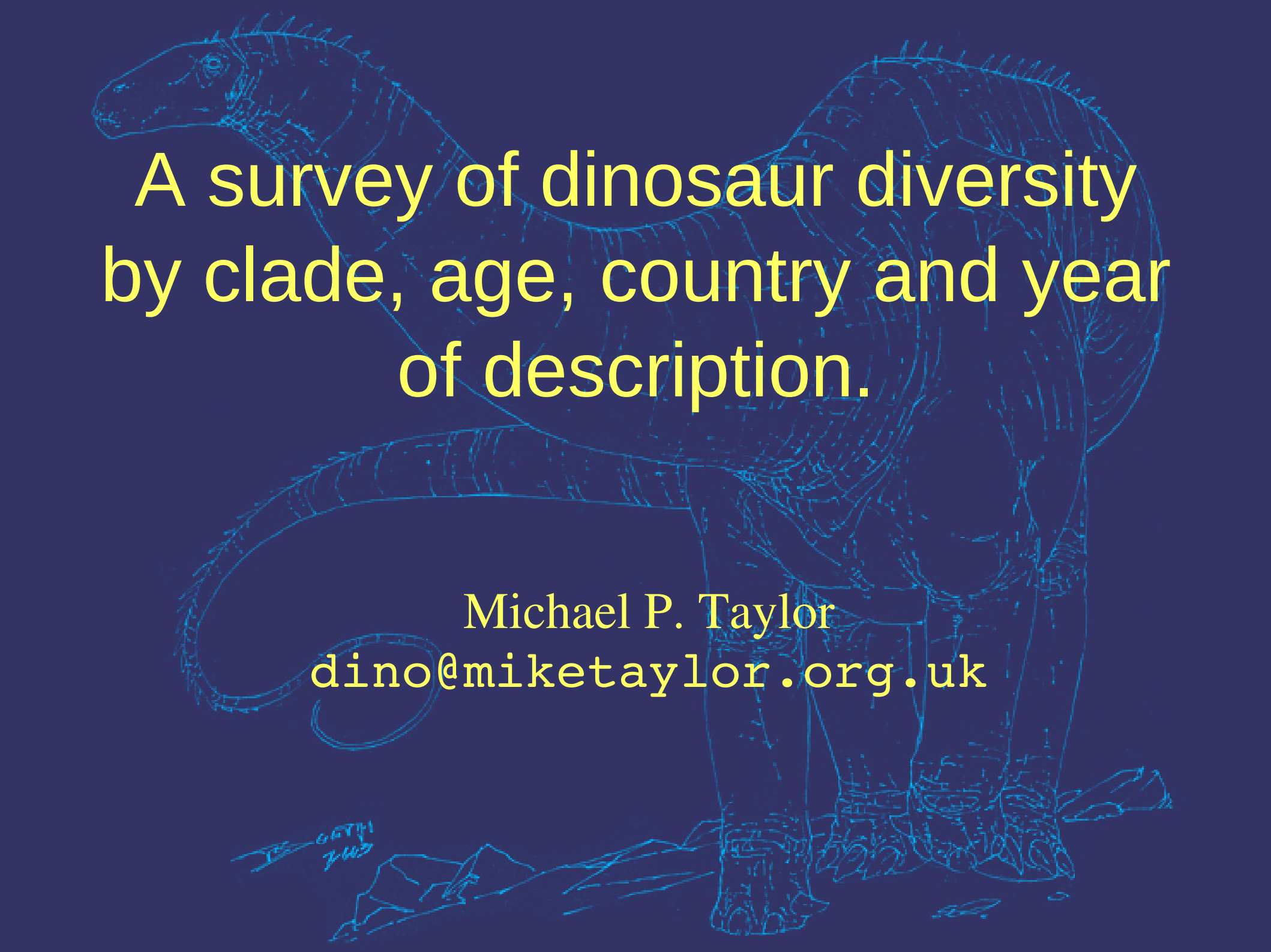

A survey of dinosaur diversity by clade, age, country and year of description.

Michael P. Taylor
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Introduction

- Understanding dinosaur diversity is essential for understanding Mesozoic ecosystems.
- There has been relatively little work in this area.
- The main contributions have all been from Dodson and his collaborators (with another to come at SVP)
- They have not analysed the record in great detail.
- The present study analyses diversity data (genus names, ages, dates, countries of origin and relationships) in four different ways.

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- The present study analyses diversity data (genus names, ages, dates, countries of origin and relationships) in four different ways.

=> Stand by for lots of numbers!

Observed and actual diversity

The diversity figures we have (“observed diversity”) are the result of a sequence of chances:

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- Which found fossils have been collected?
- Which collected fossils have been prepared?
- Which prepared fossils have been studied?

Materials and methods

- Database contains dinosaur genera generally considered valid as at the end of 2001.
- Aves *sensu* Chiappe is omitted from the database: Clade (*Archaeopteryx* + modern birds)
- Analysis program is Free (GNU GPL), and will be made available once the findings have been published.
- The program DOES NOT run a cladistic analysis: it uses a specified phylogeny, an uncontroversial consensus.

Controversy over dinosaur genera

- Dinosaur genera are subject to argument!
  - *Saurophaganax* is considered by some to be merely a big *Allosaurus*.
  - Others think *Allosaurus* should be split into multiple genera.
- Every genus is ultimately a judgement call.
- The database can only ever be a “best approximation” to reality.
- My policy: DON'T GET INVOLVED. I accept the consensus view uncritically.

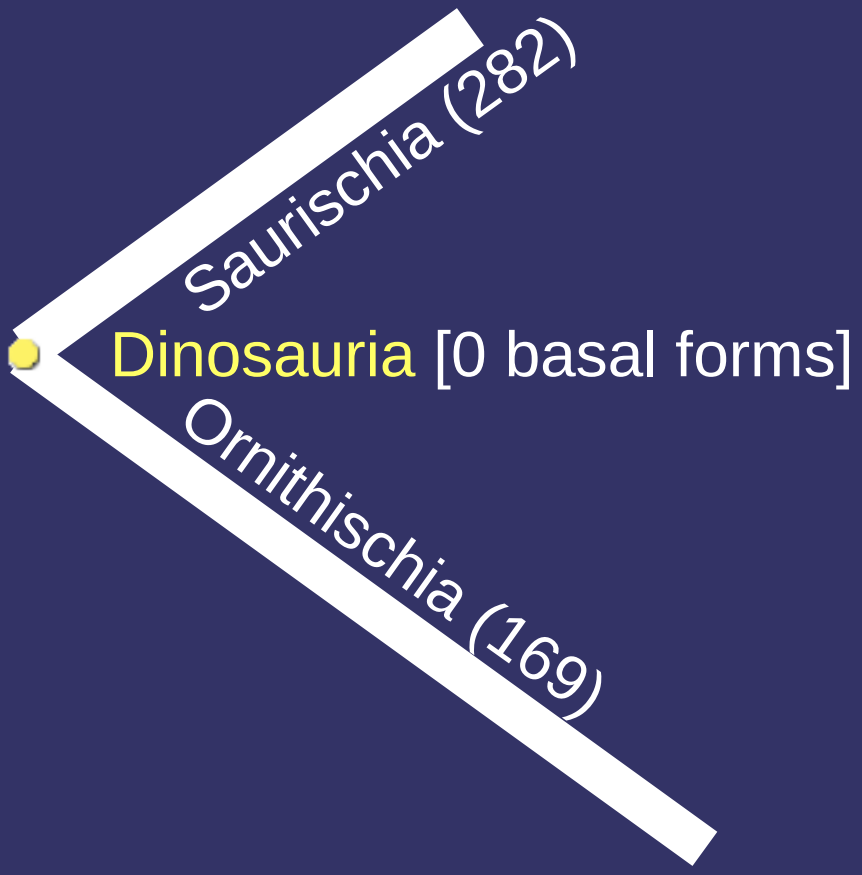
The four analyses

1. Phylogenetic. Genus counts aggregated up the tree to high-level nodes.
2. Timeline. Genera counted by the earliest geological age in which they occurred, and aggregated up to epoch and period.
3. Geographical. Genera counted by country of discovery, and aggregated up to continent.
4. Historical. Genera counted by year of naming, and aggregated up to decade.

Results 1: number of genera by clade

- Dinosauria (451 genera)

Results 1: number of genera by clade



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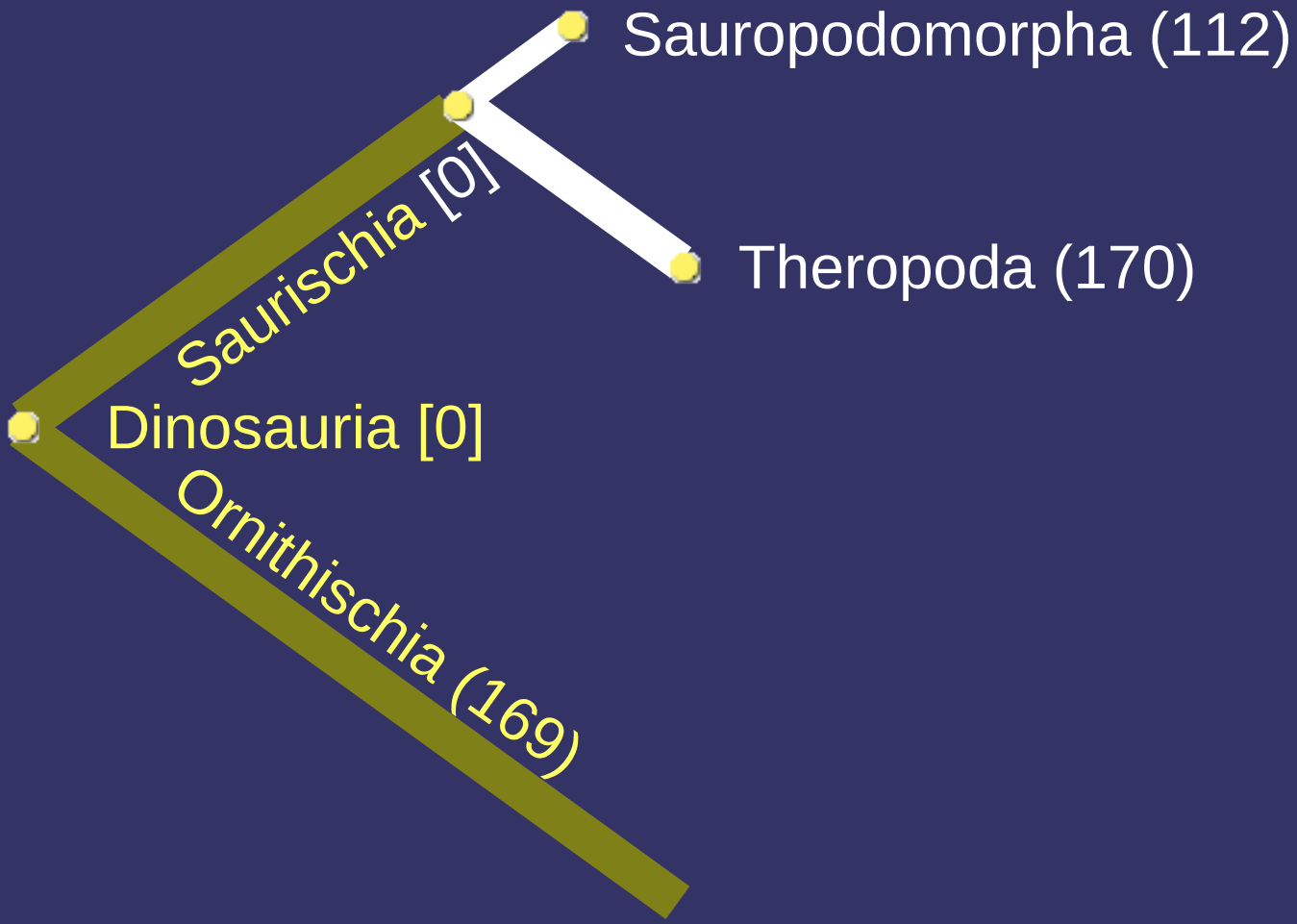

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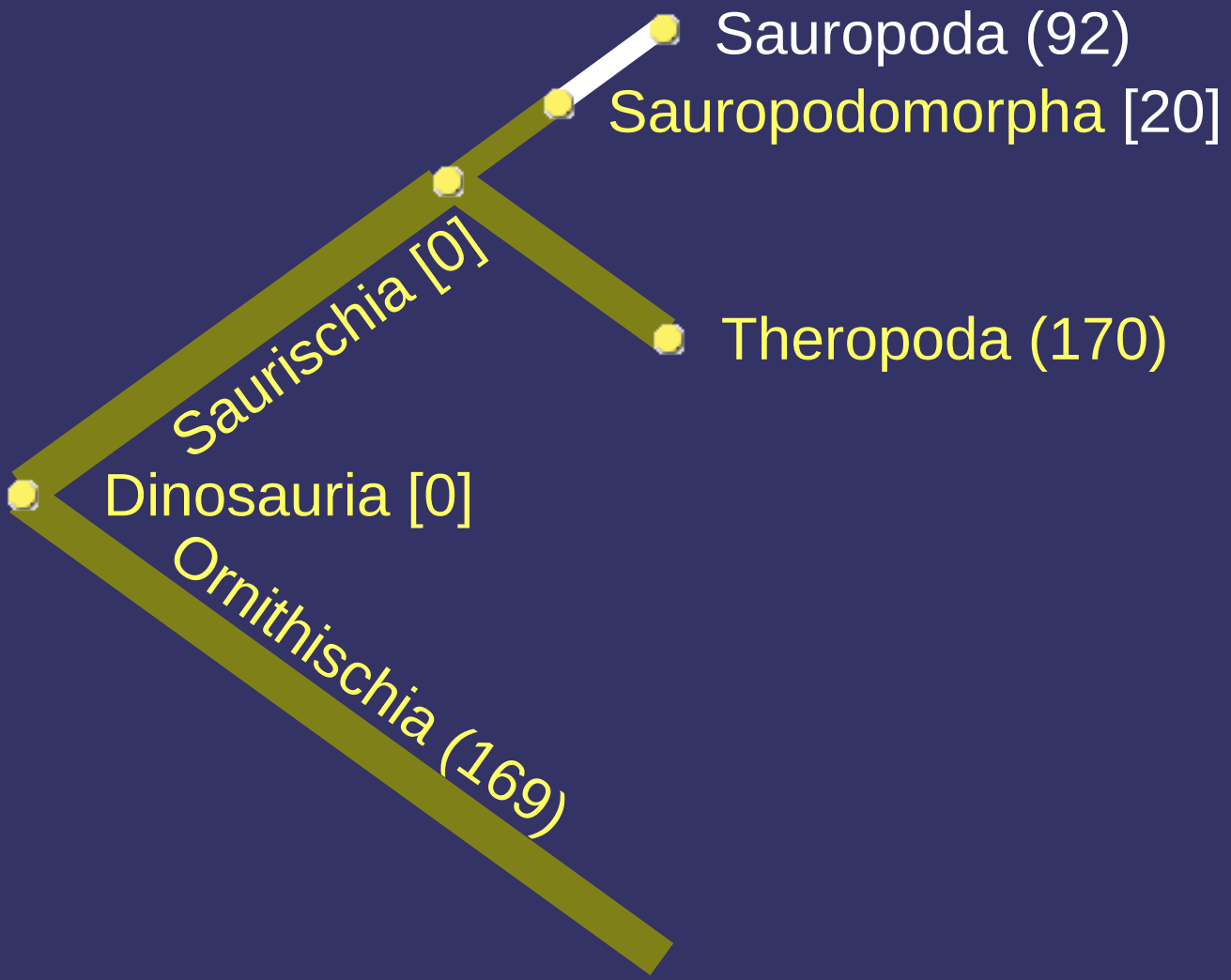

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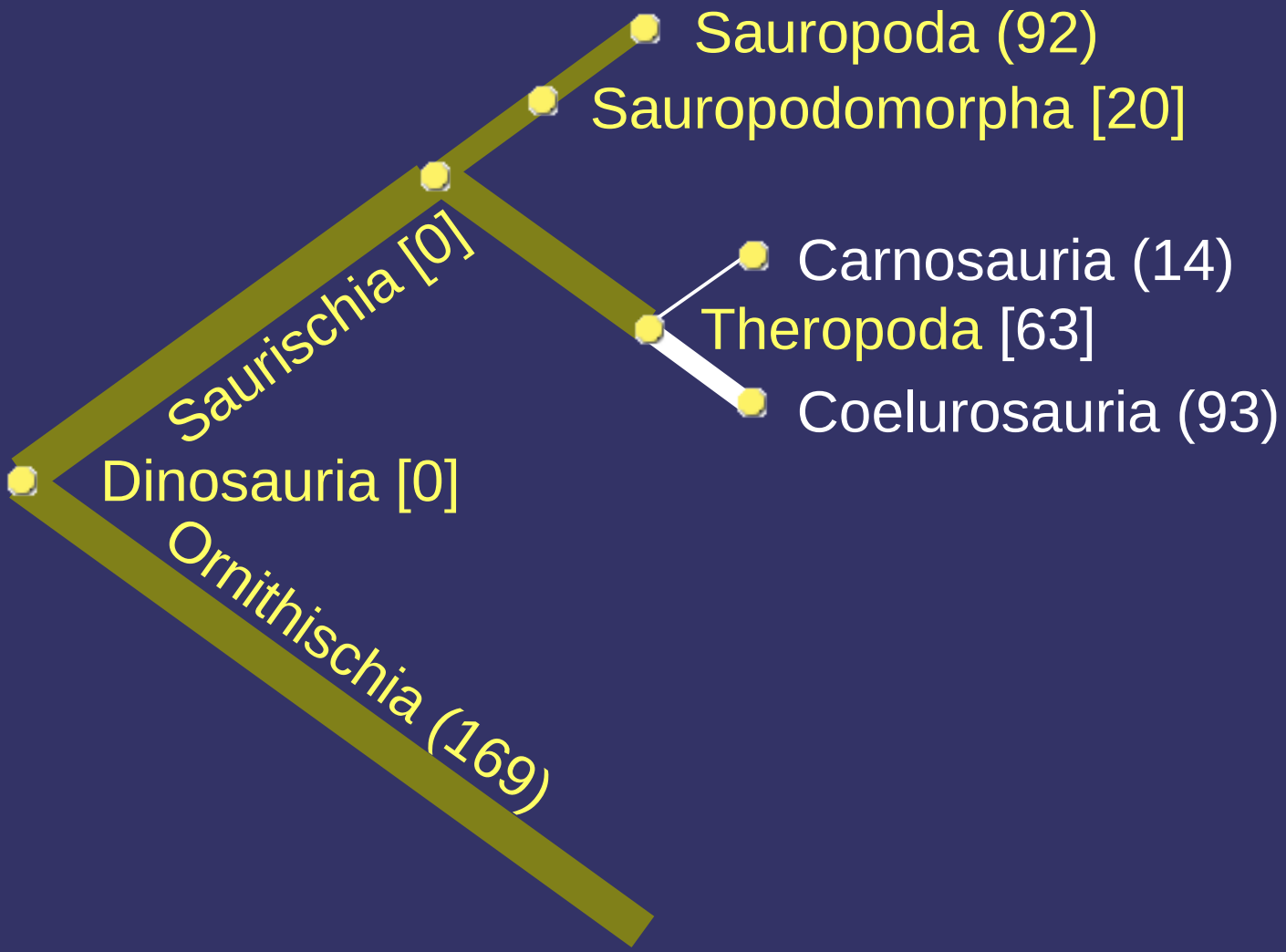

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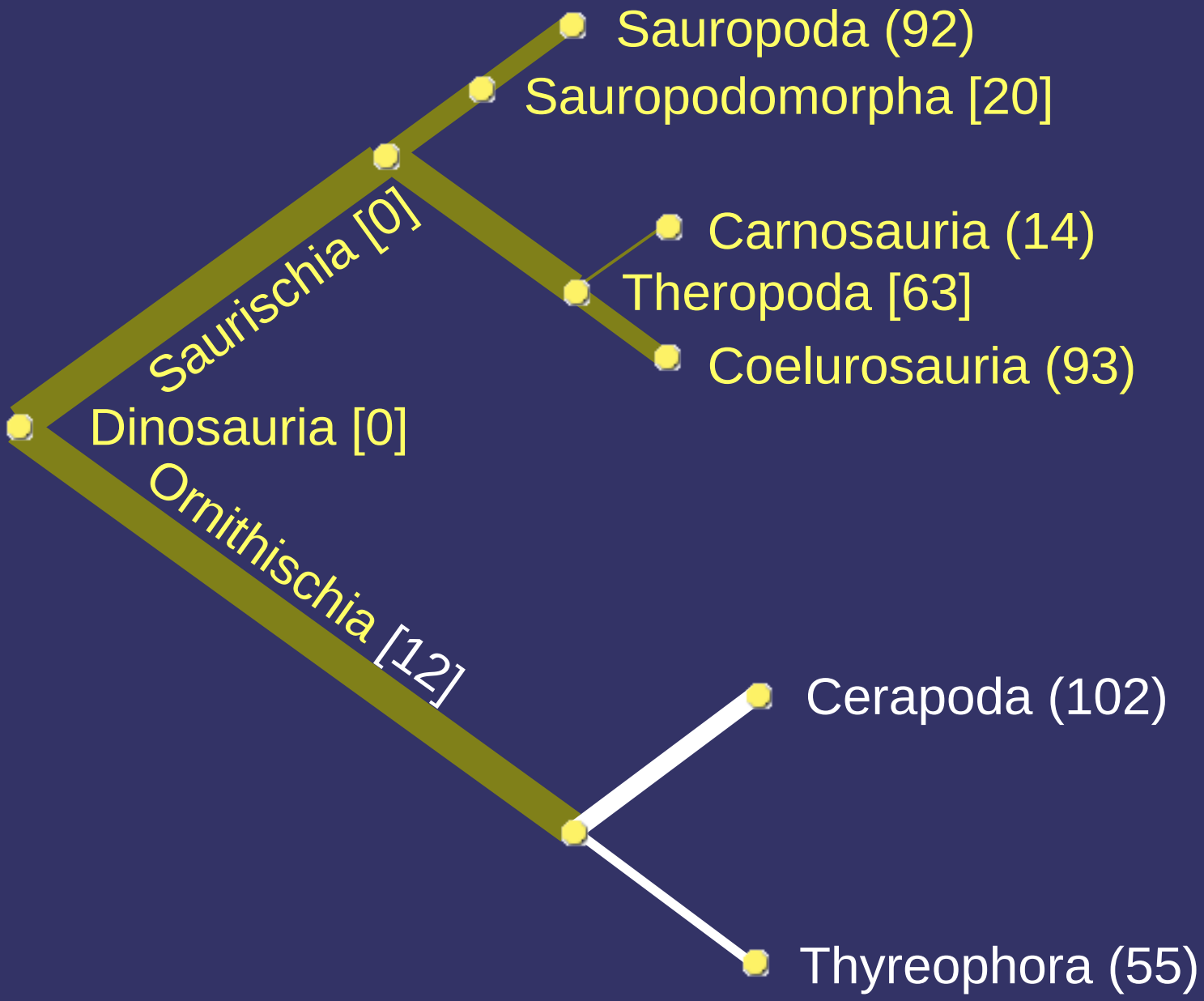

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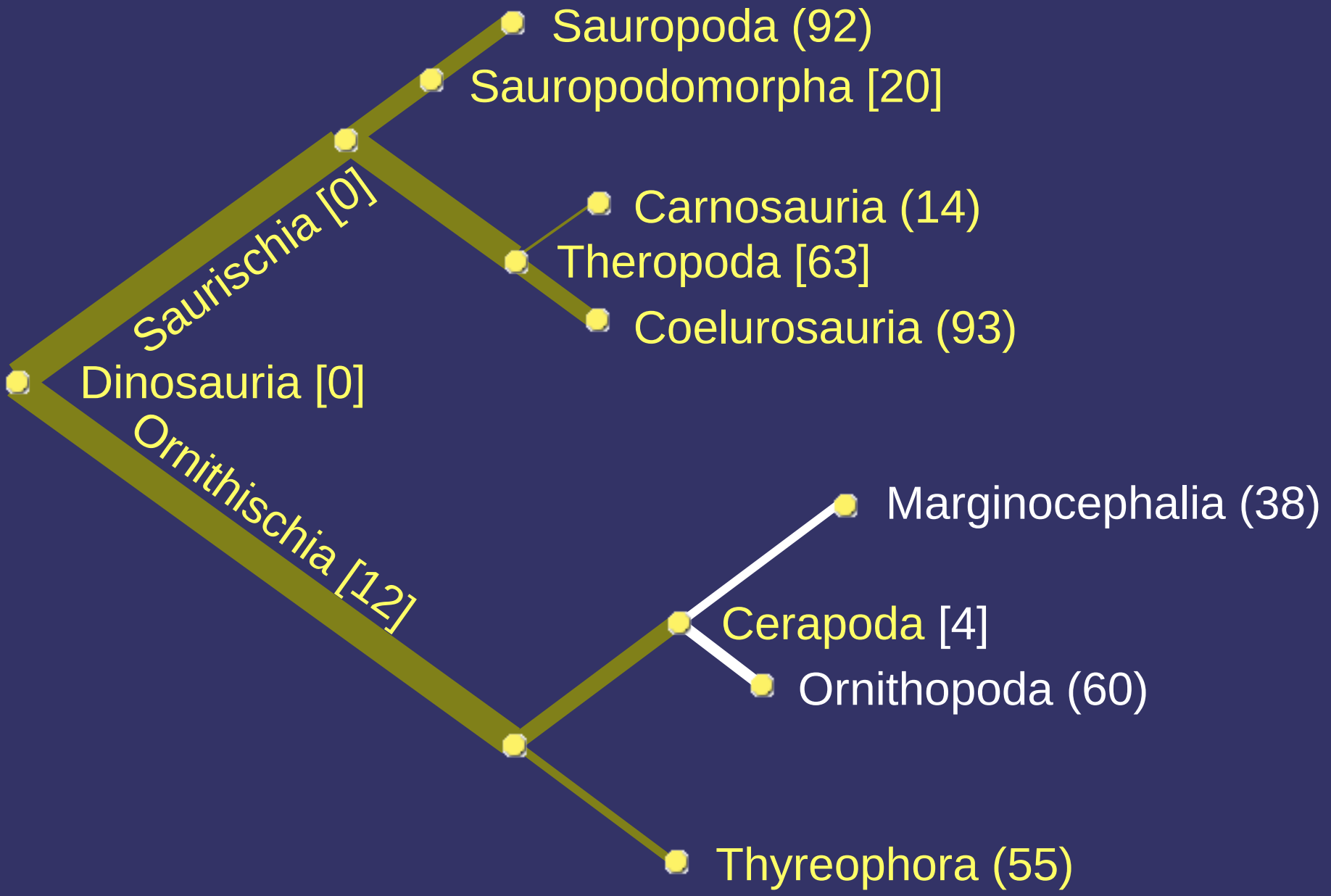

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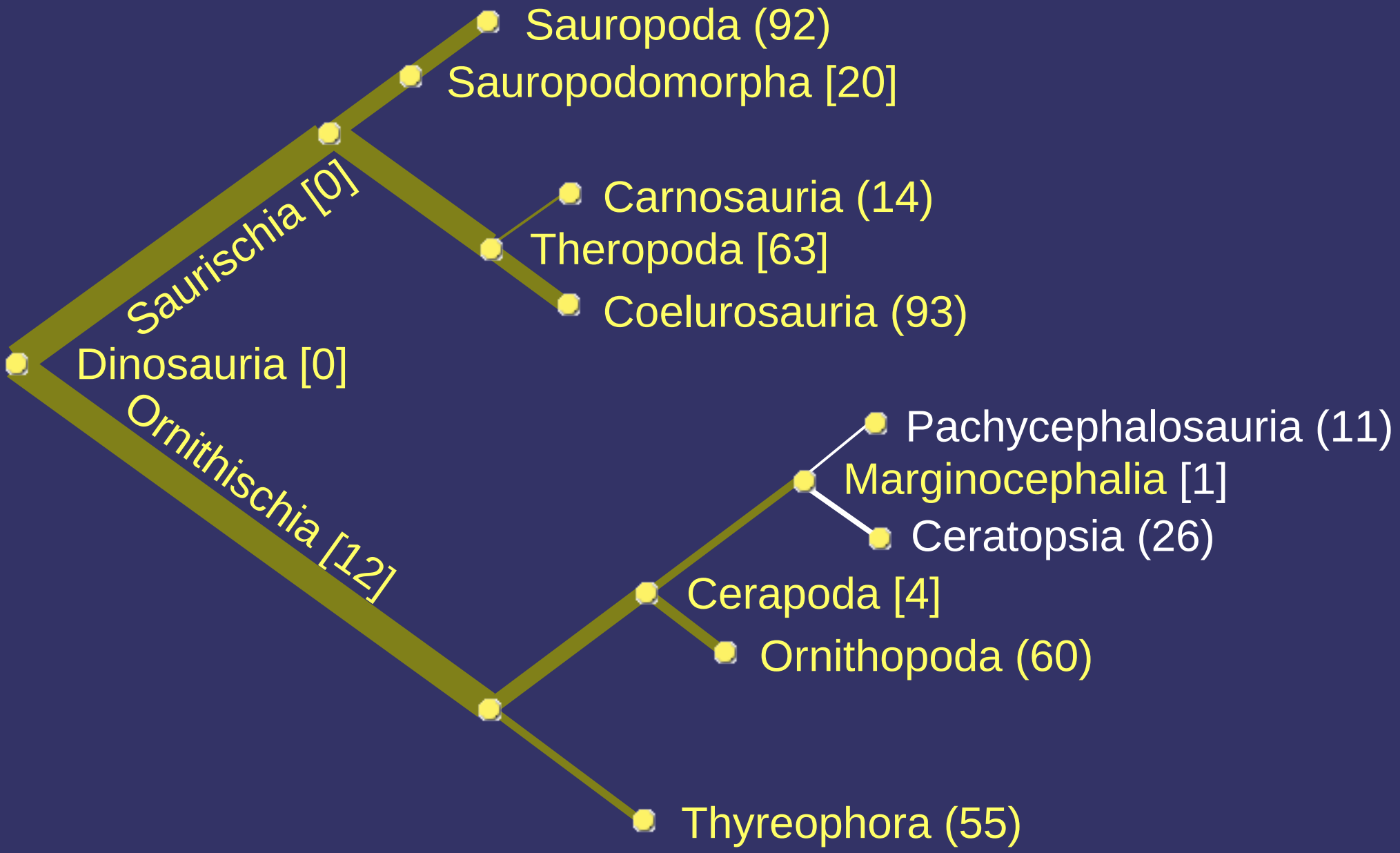

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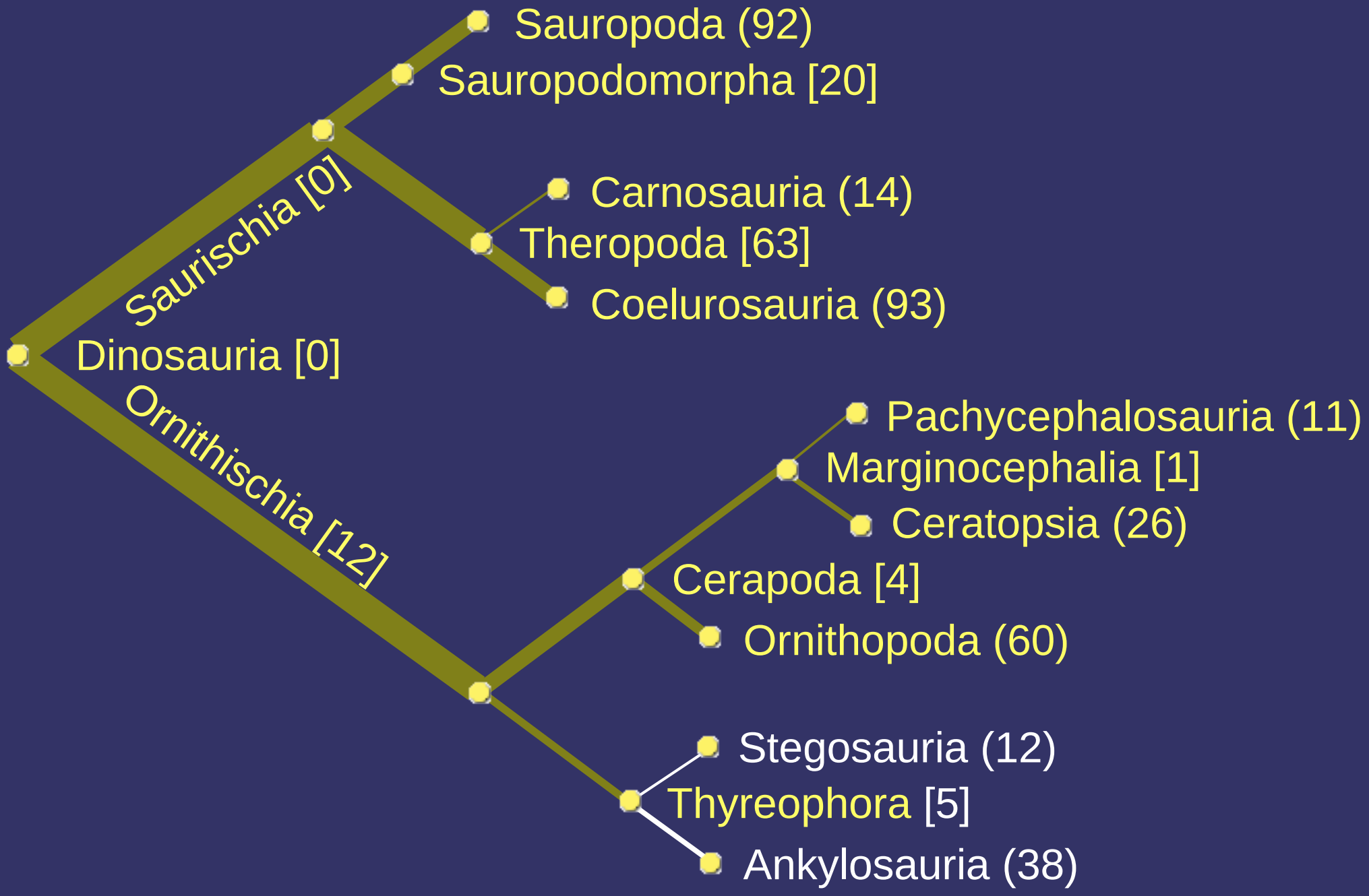

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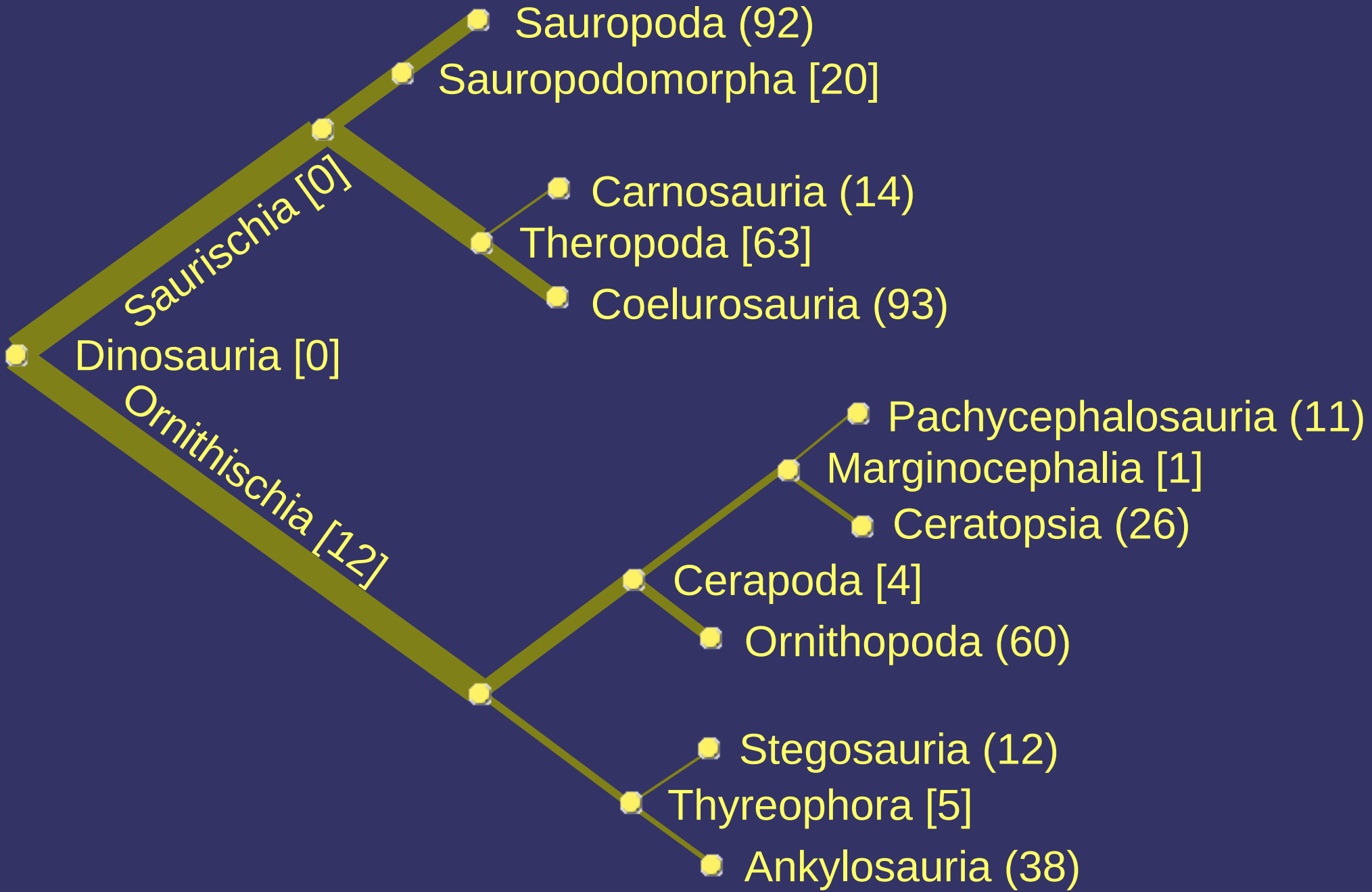

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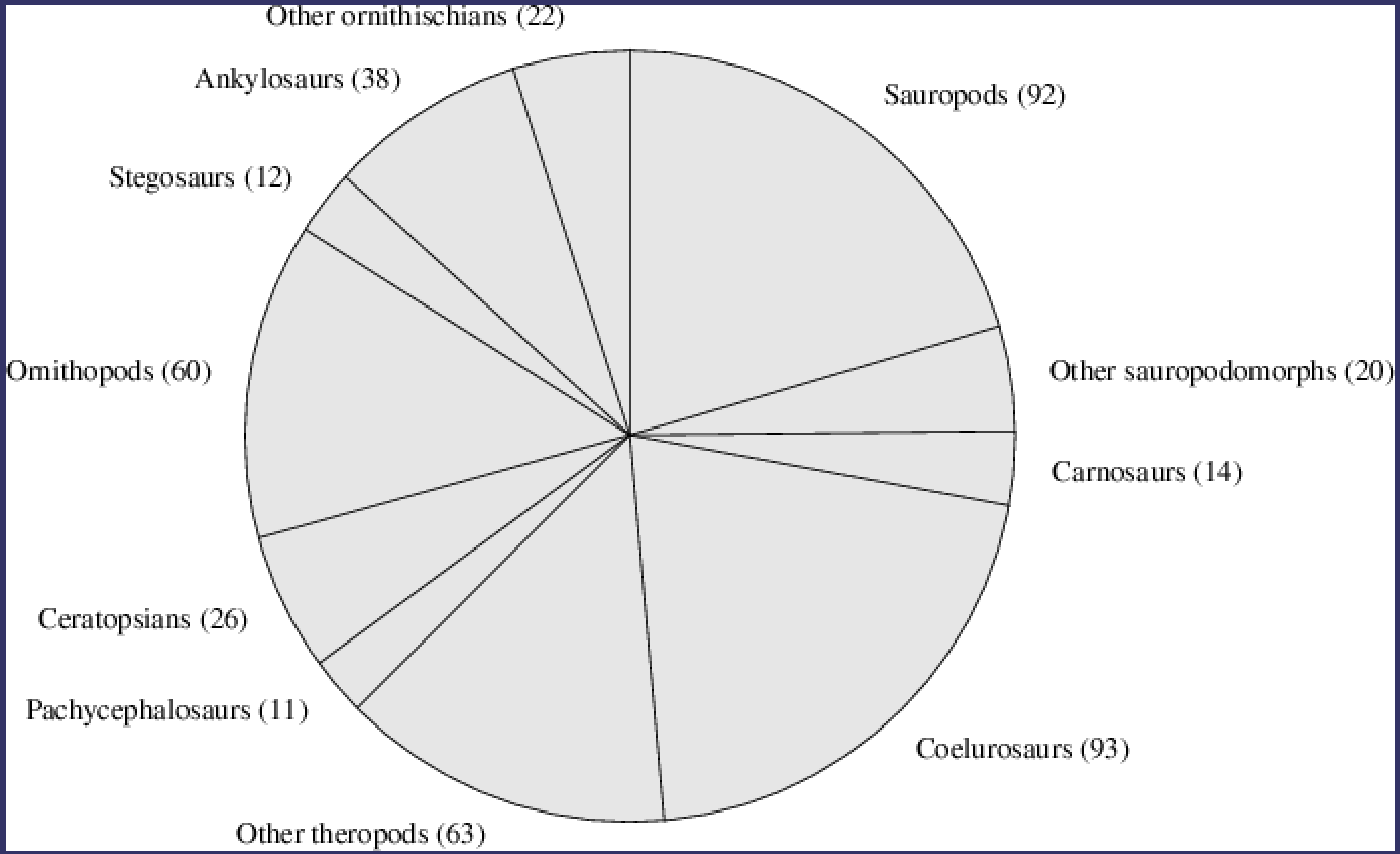

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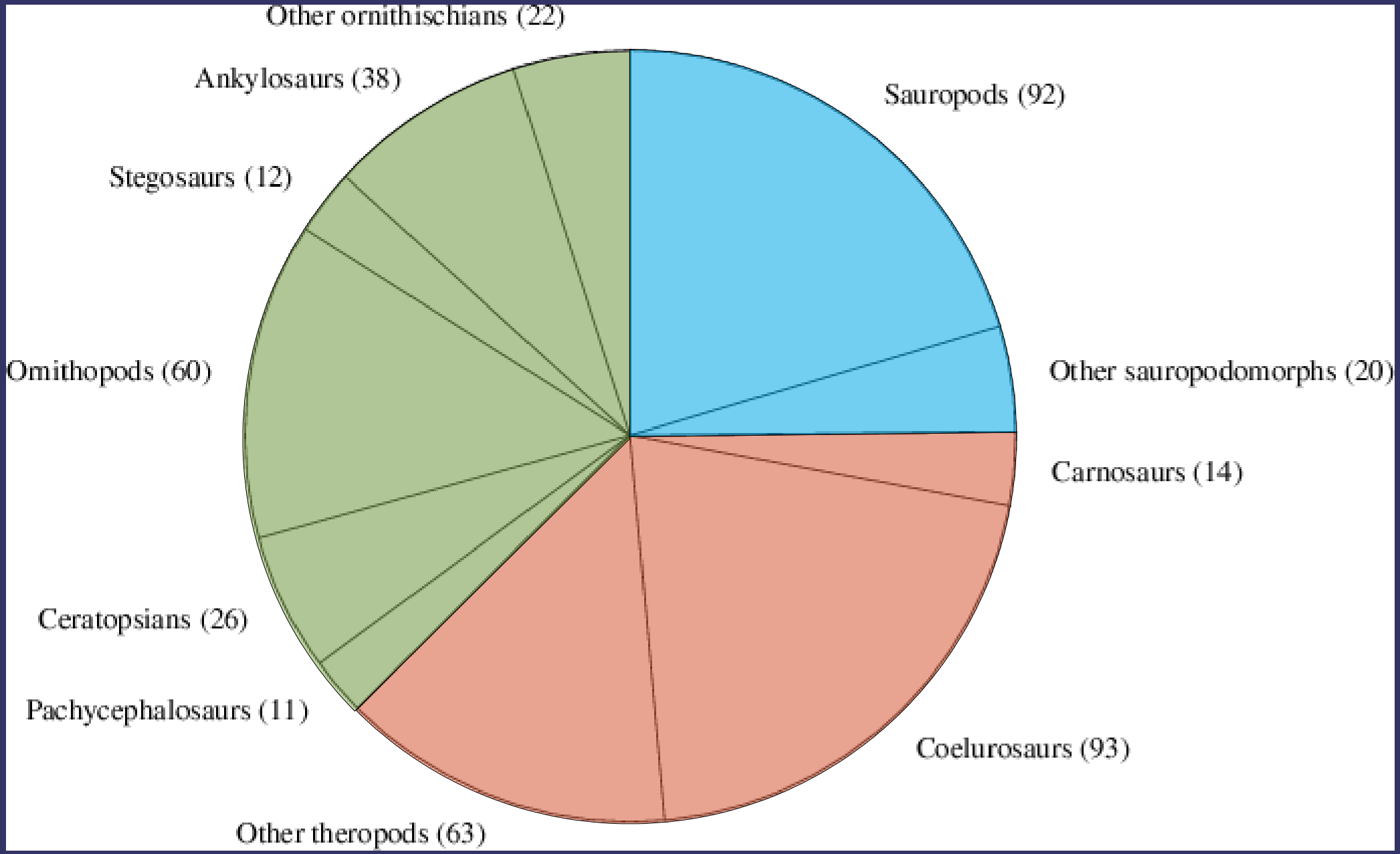

Observations on clade diversity

- Saurischian genera outnumber ornithischians by five to three (282 to 169)
- Theropods alone outnumber ornithischians!
- This is surprising given that theropods all look the same ("teeth at one end, a tail at the other and a pair of legs sticking down in the middle.")
- Ornithischians are much more varied in body plan (consider *Triceratops*, *Parasaurolophus* and *Stegosaurus*).

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=> The ornithischian renaissance is overdue!

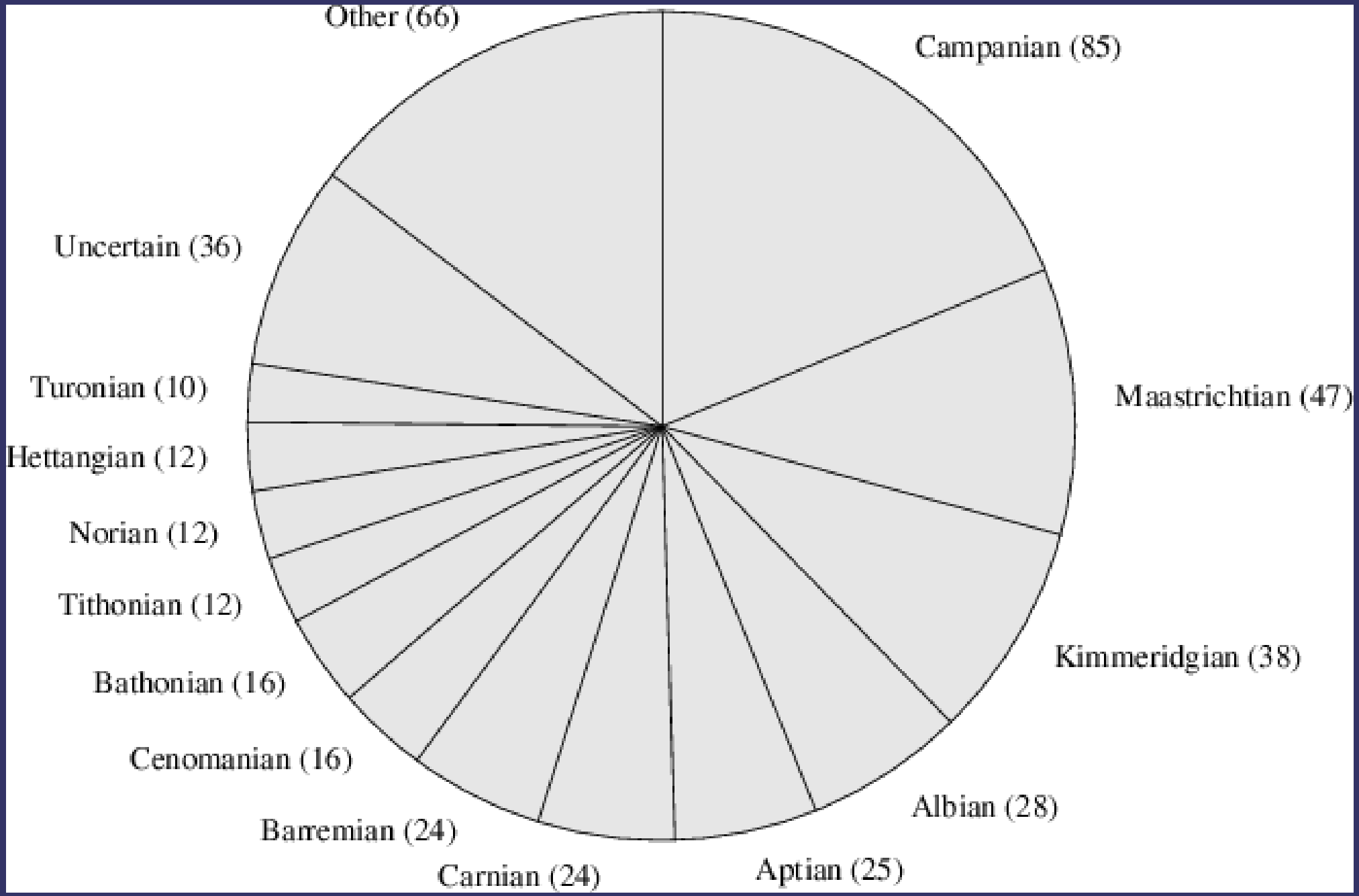
Carnivores and Herbivores

- All sauropodomorphs and ornithischians were herbivorous (perhaps excepting a few very basal forms.)
- Among theropods, ornithomimosaurs and therizinosaurs were probably herbivorous or omnivorous.
- This leaves 151 carnivorous genera (non-ornithimimosaur, non-therizinosaur theropods)
- This is one third of the total 451 genera, which seems a high proportion.

Results 2: genera by geological age

Period	Epoch	Age	Definition (Mya)	Number of Genera	Uncertain Age	
Triassic				38		
	Late Triassic			38	1	I
		Carnian	227.4-220.7	24		IIIIII IIIII I I I III
		Norian	220.7-209.6	12		IIIIII III
		Rhaetian	209.6-205.7	1		I
Jurassic				124		
	Early Jurassic			29	4	III
		Hettangian	205.7-201.9	12		IIIIII III
		Sinemurian	201.9-195.3	4		III
		Pliensbachian	195.3-189.6	3		III
		Toarcian	189.6-180.1	6		IIII
	Middle Jurassic			34	4	III
		Aalenian	180.1-176.5	2		II
		Bajocian	176.5-169.2	3		III
		Bathonian	169.2-164.4	16		IIIIII IIIII I
		Callovian	164.4-159.4	9		IIIIII
	Late Jurassic			61	3	III
		Oxfordian	159.4-154.1	8		IIIIII
		Kimmeridgian	154.1-150.7	38		IIIIII IIIII I I I III IIIIIIIIII
		Tithonian	150.7-144.2	12		IIIIII III
Cretaceous				289		
	Early Cretaceous			102	10	IIIIII I
		Berriasian	144.2-137.0	2		II
		Valanginian	137.0-132.0	4		III
		Hauterivian	132.0-127.0	9		IIIIII
		Barremian	127.0-121.0	24		IIIIII IIIII I I I III
		Aptian	121.0-112.2	25		IIIIII IIIII I I I III
		Albian	112.2-98.9	28		IIIIII IIIII I I I III I I
	Late Cretaceous			187	14	IIIIII IIIII
		Cenomanian	98.9-93.5	16		IIIIII IIIII I
		Turonian	93.5-89.9	10		IIIIII I
		Coniacian	89.9-85.8	7		IIIII
		Santonian	85.8-83.5	8		IIIIII
		Campanian	83.5-71.0	85		IIIIII IIIII I I I III IIIIIIIIIIIIIII IIIII I IIIII IIIIIIIIIIIII I
		Maastrichtian	71.0-65.0	47		IIIIII IIIII I I I III IIIIIIIIIIIII I

Most productive ages



Early dinosaur diversification

- Dinosaurs appear to have diversified swiftly in the Carnian, the first age in which they appeared.
- 24 Carnian genera in total:
  - 6 ornithischians (all basal)
  - 4 sauropodomorphs (all "prosauropods")
  - 14 theropods
    - 8 basal
    - 6 neotheropods, none of them tetanuran.
- 12 more new genera in the Norian, including the earliest sauropod, *Isanosaurus*.

Diversity trends through time

- 38 Triassic genera in 21.7 million years from Carnian.

  => genus density (GD) of 1.75 genera per million years.

- 124 Jurassic genera in 61.5 million years.

  => GD = 2.0

- 289 Cretaceous genera in 79.2 million years.

  => GD = 3.65

- General trend in *observed* diversity is towards increasing diversity through time.

- Bias is partly because older fossils have more time in which to be destroyed by processes such as erosion.

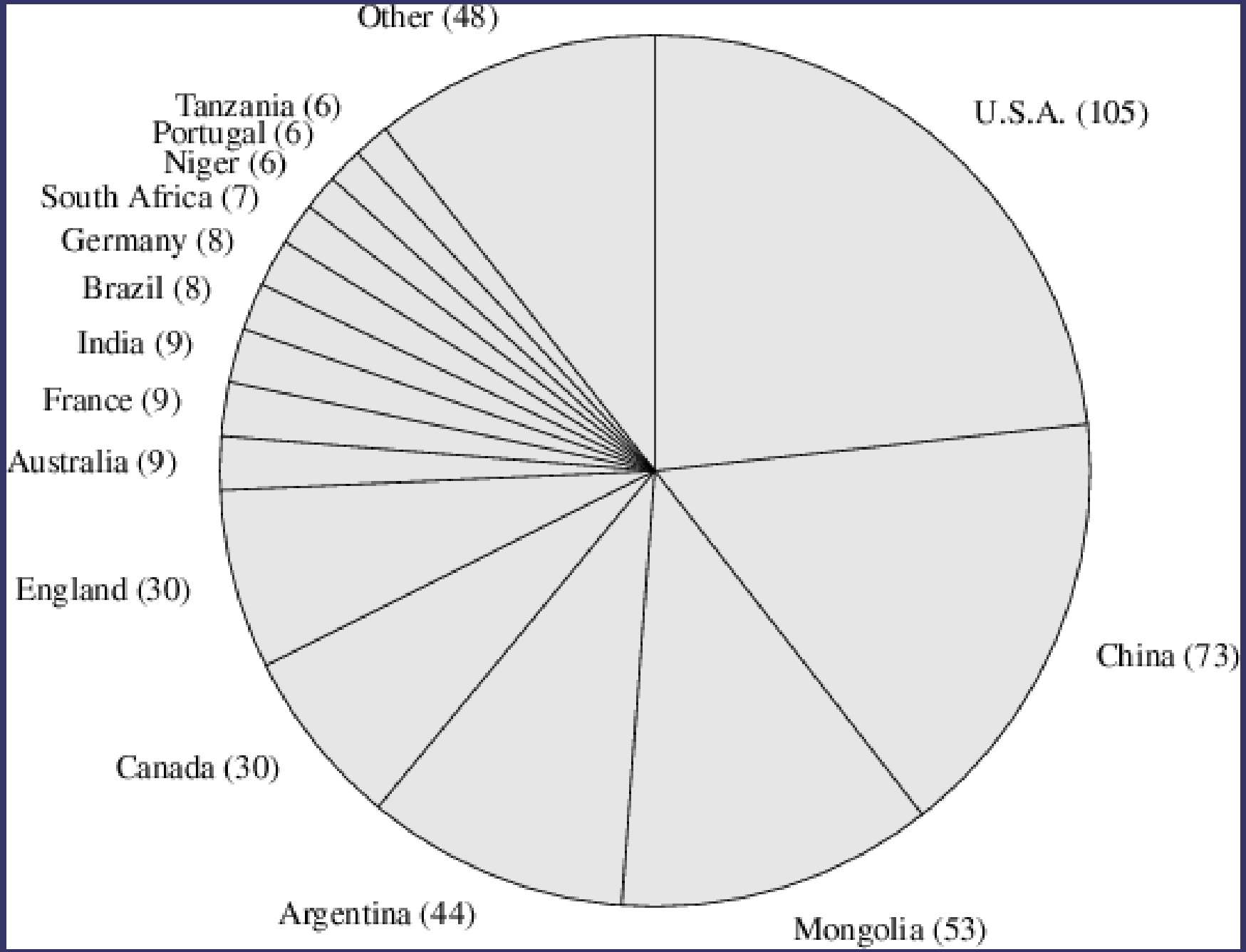
Results 2a: genus density by geological age

Age	Definiton (Mya)	Duration (Ma)	Number of Genera	Genus Density	
Induan	248.2-244.8	3.40	0	0.00	
Olenekian	244.8-241.7	3.10	0	0.00	
Anisian	241.7-234.3	7.40	0	0.00	
Ladinian	234.3-227.4	6.90	0	0.00	
Carnian	227.4-220.7	6.70	24	3.58	
Norian	220.7-209.6	11.10	12	1.08	
Rhaetian	209.6-205.7	3.90	1	0.26	
Hettangian	205.7-201.9	3.80	12	3.16	
Sinemurian	201.9-195.3	6.60	4	0.61	
Pliensbachian	195.3-189.6	5.70	3	0.53	
Toarcian	189.6-180.1	9.50	6	0.63	
Aalenian	180.1-176.5	3.60	2	0.56	
Bajocian	176.5-169.2	7.30	3	0.41	
Bathonian	169.2-164.4	4.80	16	3.33	
Callovian	164.4-159.4	5.00	9	1.80	
Oxfordian	159.4-154.1	5.30	8	1.51	
Kimmeridgian	154.1-150.7	3.40	38	11.18	
Tithonian	150.7-144.2	6.50	12	1.85	
Berriasian	144.2-137.0	7.20	2	0.28	
Valanginian	137.0-132.0	5.00	4	0.80	
Hauterivian	132.0-127.0	5.00	9	1.80	
Barremian	127.0-121.0	6.00	24	4.00	
Aptian	121.0-112.2	8.80	25	2.84	
Albian	112.2- 98.9	13.30	28	2.11	
Cenomanian	98.9- 93.5	5.40	16	2.96	
Turonian	93.5- 89.9	3.60	10	2.78	
Coniacian	89.9- 85.8	4.10	7	1.71	
Santonian	85.8- 83.5	2.30	8	3.48	
Campanian	83.5- 71.0	12.50	85	6.80	
Maastrichtian	71.0- 65.0	6.00	47	7.83	

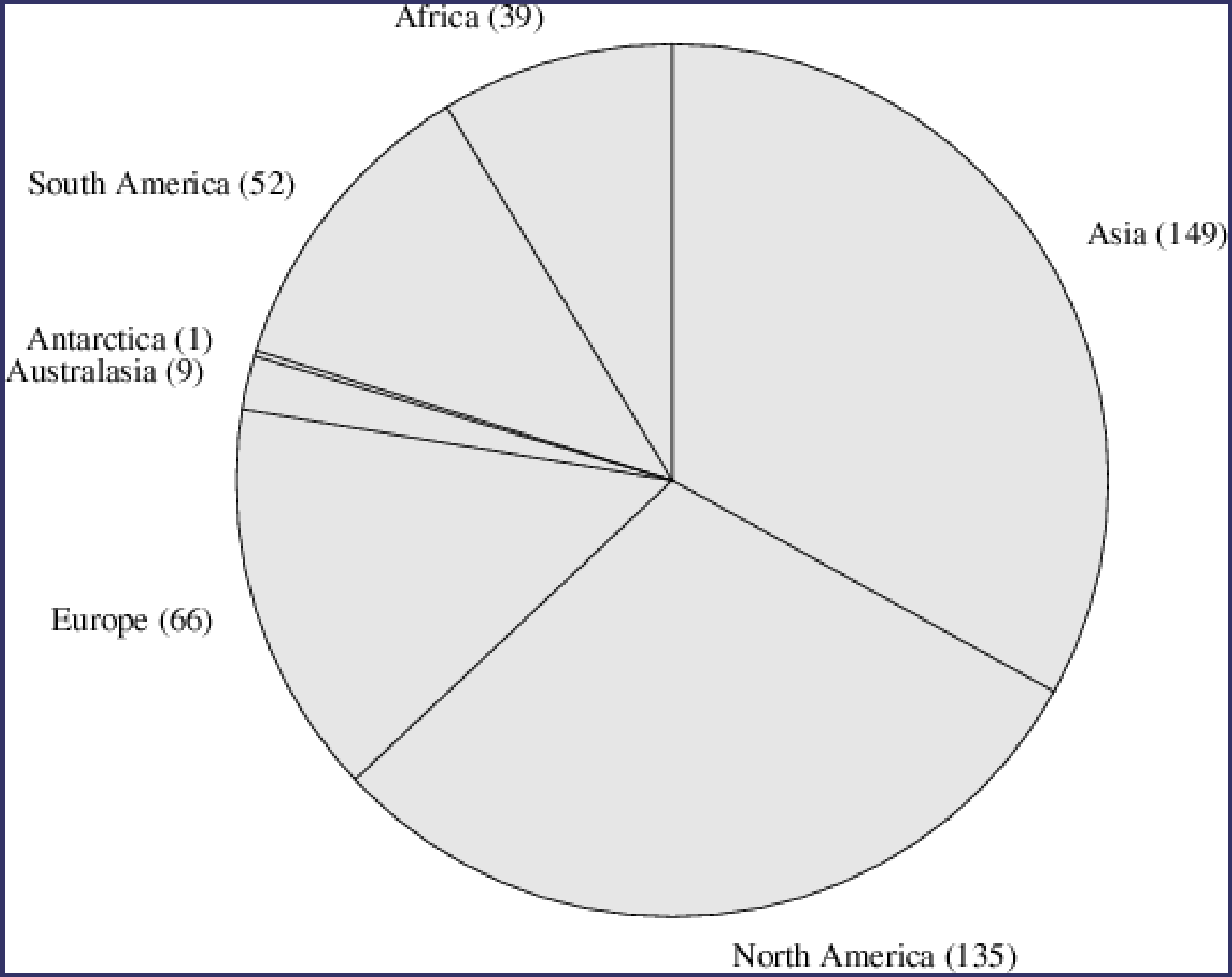
Peaks in dinosaur diversity

- Three ages are much more diverse than the others:
  - Kimmeridgian: GD = 11.18
  - Maastrichtian: GD = 7.83
  - Campanian: GD = 6.80
- No other age has a GD greater than 4.0 (Barremian)
- High diversity in late Cretaceous seems to contradict Dodson 1994's assertion than diversity was declining prior to K/T.
- This seeming contradiction is probably due to coarser time resolution in the current study.

Results 3: genera by country



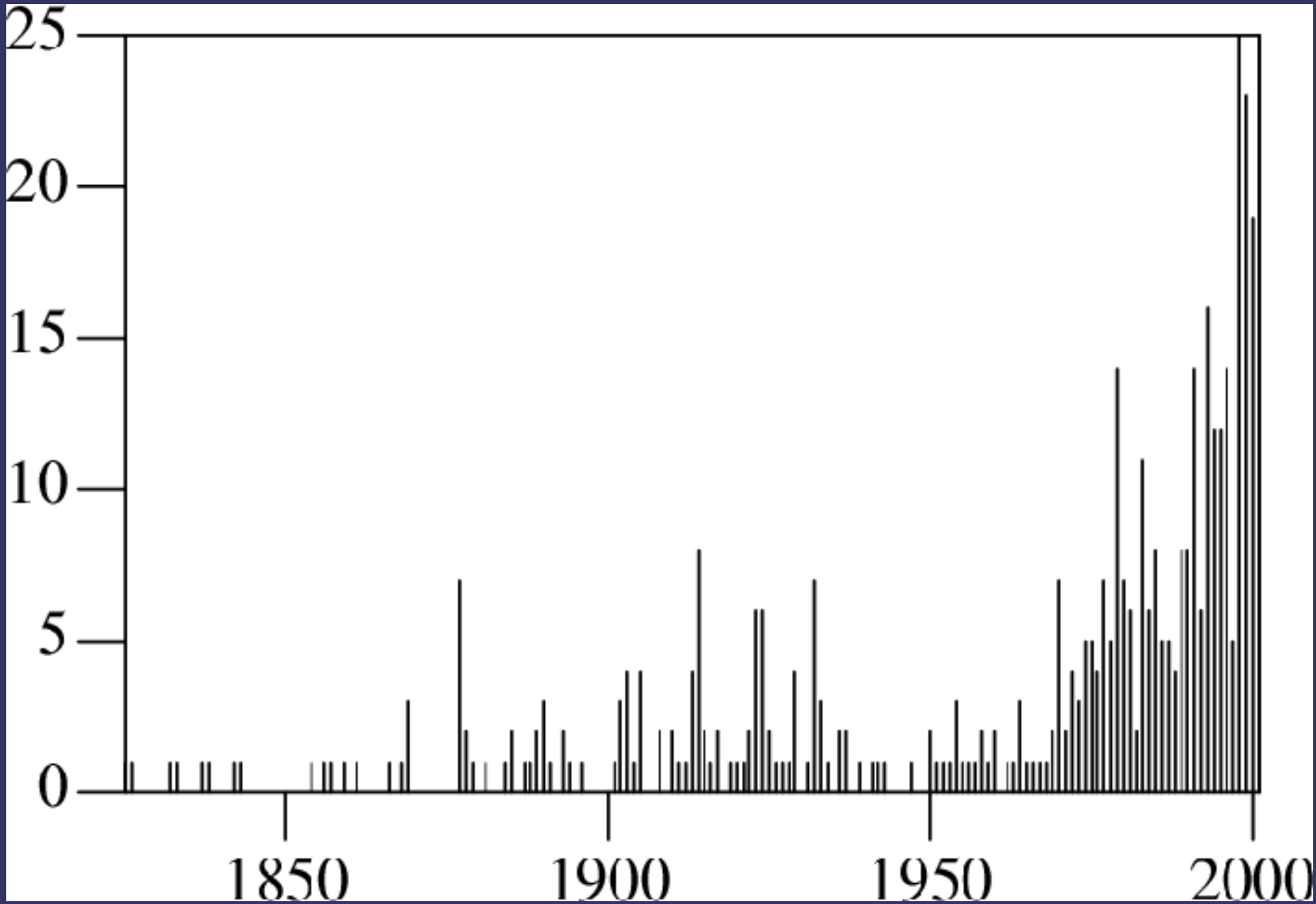
Results 3a: genera by continent



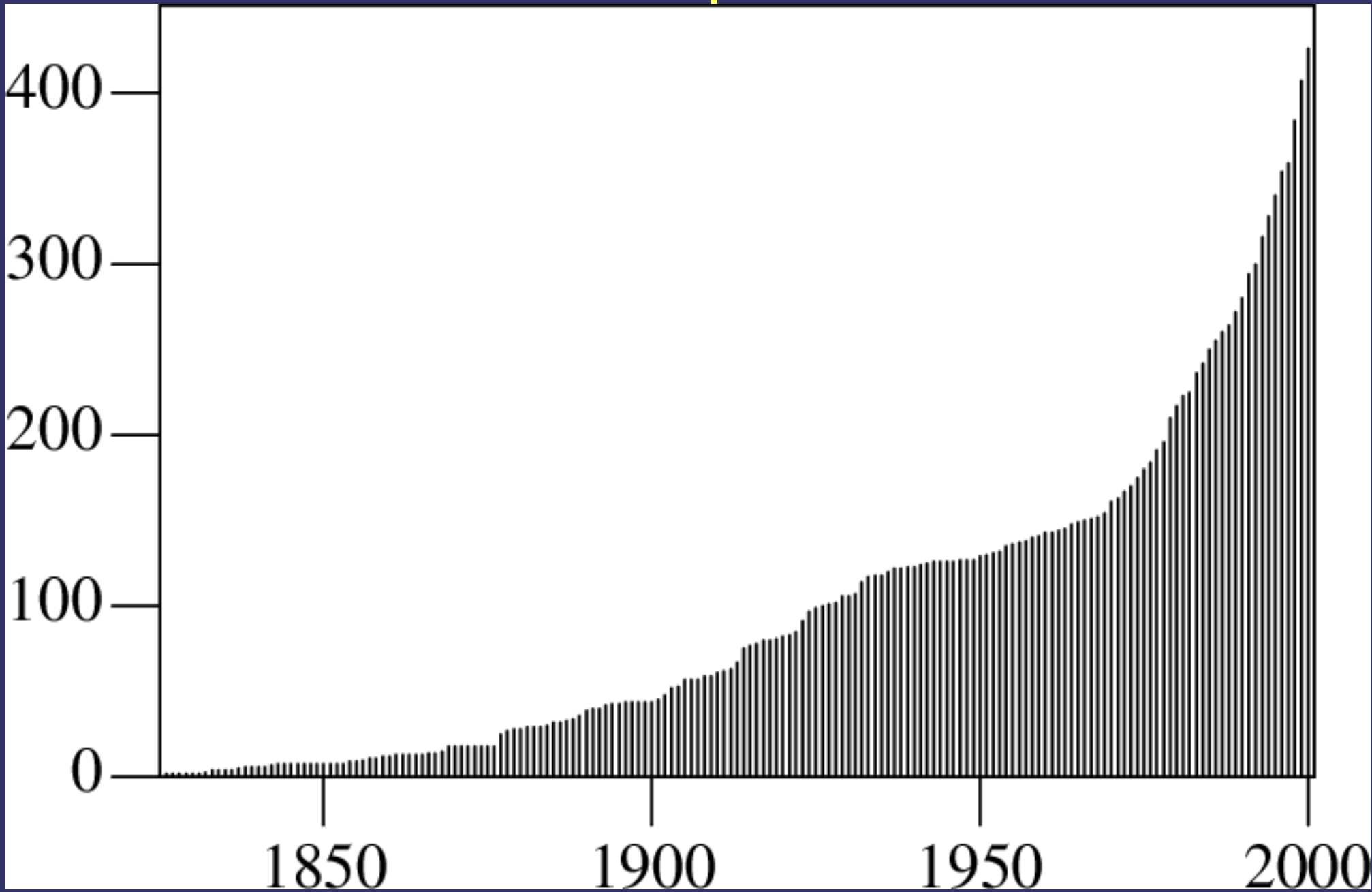
Geographical distribution in history

- Early work was in Europe: first eight genera (28 years) all European until *Massospondylus* (Lesotho, Africa) became the first non-European dinosaur in 1854.
- Europe dominated dinosaur genus counts for 65 years from 1825-1889.
- By 1890, North America had overtaken Europe, and has remained ahead ever since.
- 45-year gap between Asia's first and second dinosaurs (*Titanosaurus* in 1877; then three in 1923)
- In 1993, Asia overtook North America as most diverse continent.

Results 4: new genera by year of description



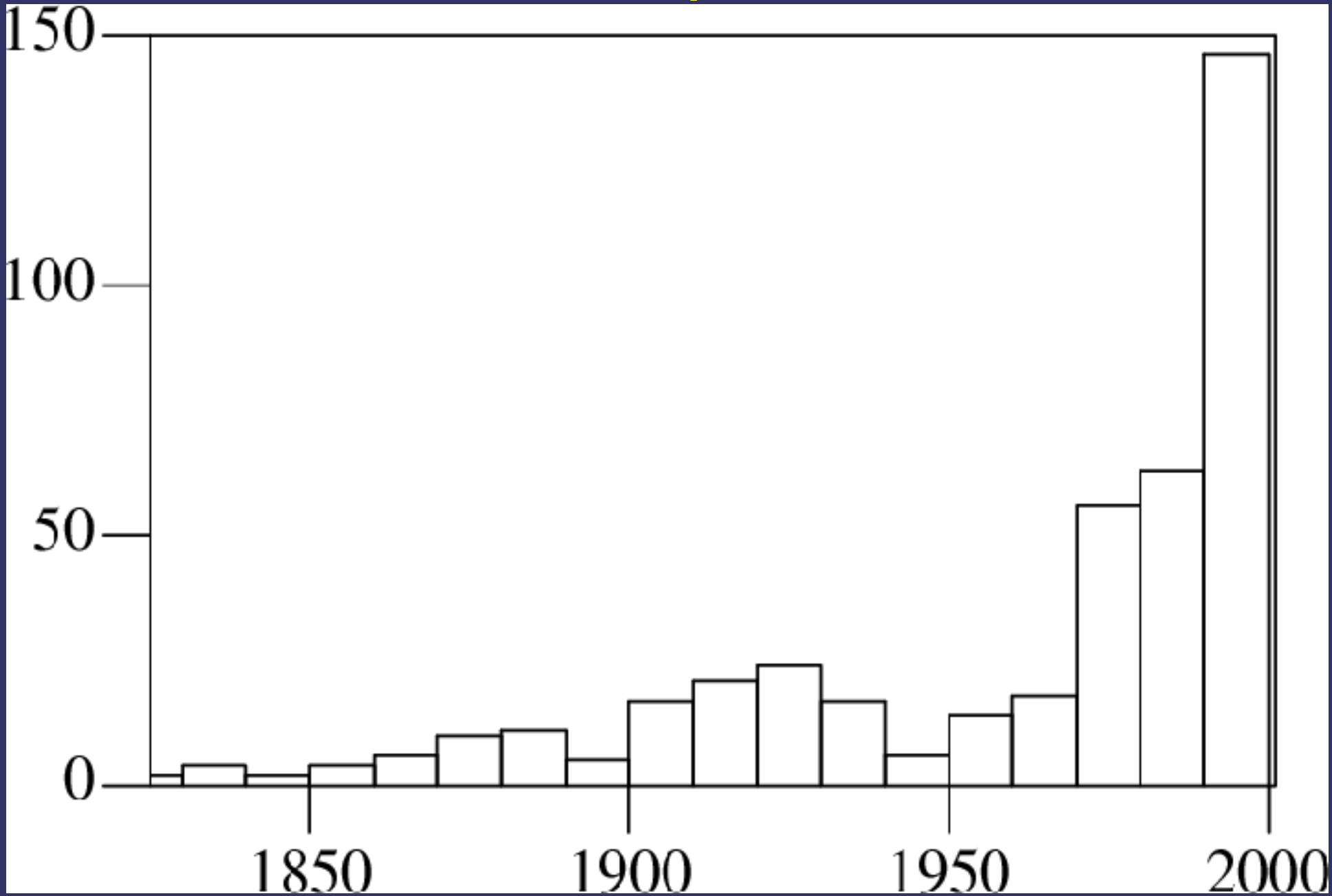
Results 4a: total genera by year of description



Observations on dinosaur naming rate

- The overall trend is very obviously towards the more rapid naming of new dinosaur genera.
- There are large fluctuations between consecutive years.
- The last year with no new dinosaurs named was 1961; the previous was 1949. So we have had new dinosaurs every year but one of the last half-century.
- It took 158 years to name the first half of the genera; and 19 years to name the rest – eight times as fast!

Results 4b: new genera by decade of description



Dinosaur naming rate by decade

- Apart from a gap in the 30s-60s, the rate of naming appears exponential.
- These four decades represent the dinosaur “dark ages” in which palaeontology was largely mammal-oriented.
- The dark ages ended in the 70s with the “Dinosaur renaissance” (Ostrom 1969, Bakker 1975)
- The 56 genera named in the 1970s outnumber all those from the preceding four decades

Discussion

- Why we count genera rather than species.
- Five reasons for diversity variations between ages and between clades.

Genus and species

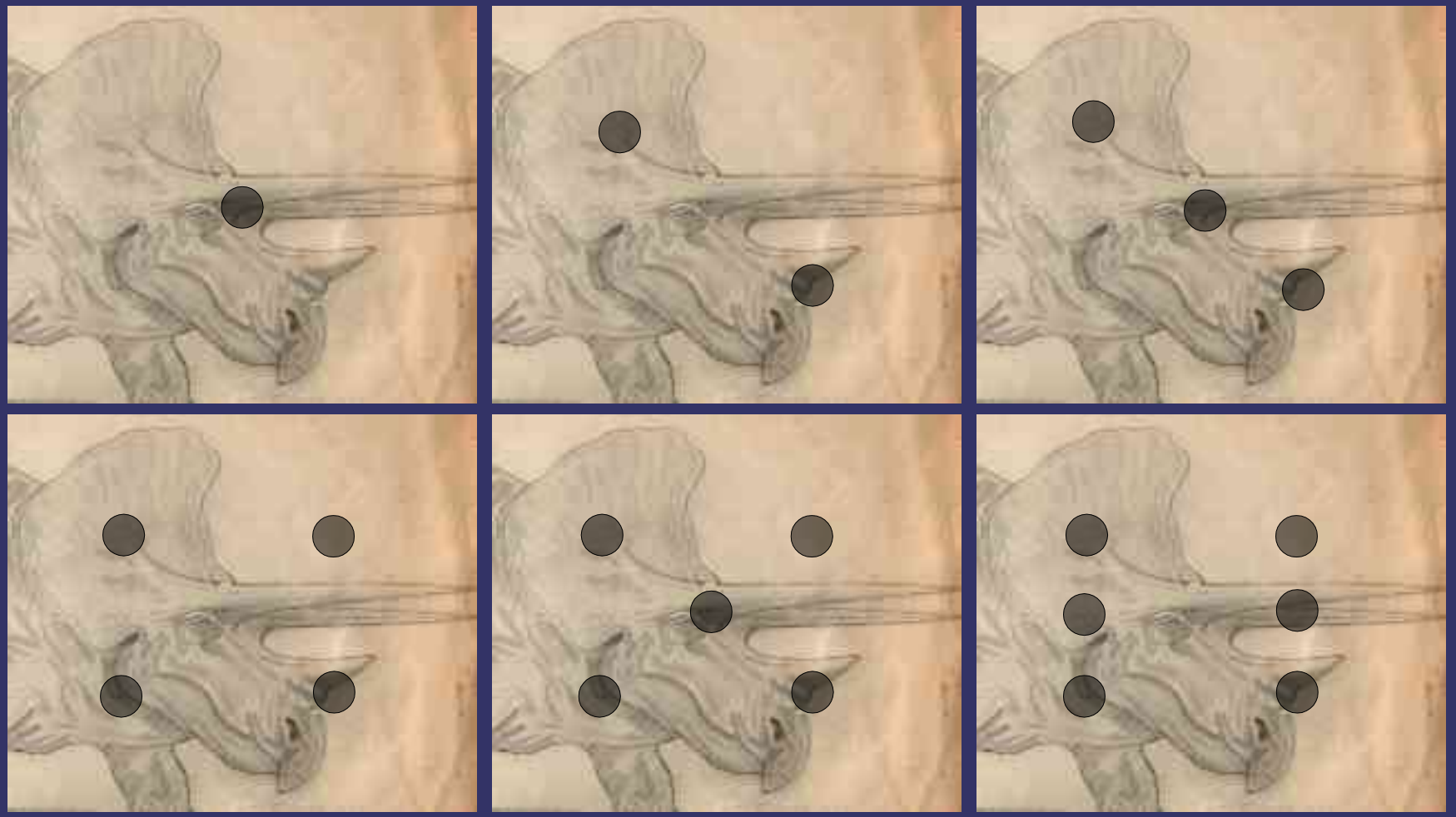
- Why does this study count genera rather then species?
- For extant organisms, species may be objectively real and genera merely a convenient abstraction.
- For extinct organisms, the opposite is more nearly true. "Biological concept" of species is useless.
- No-one agrees about the assignment of dinosaur specimens to species, but there is *some* consensus concerning genera.

Dinosaur species – a case study: *Triceratops*

- Ten species (Hatcher et al. 1907)

Dinosaur species – a case study: *Triceratops*

- No, six species (Lull 1933)



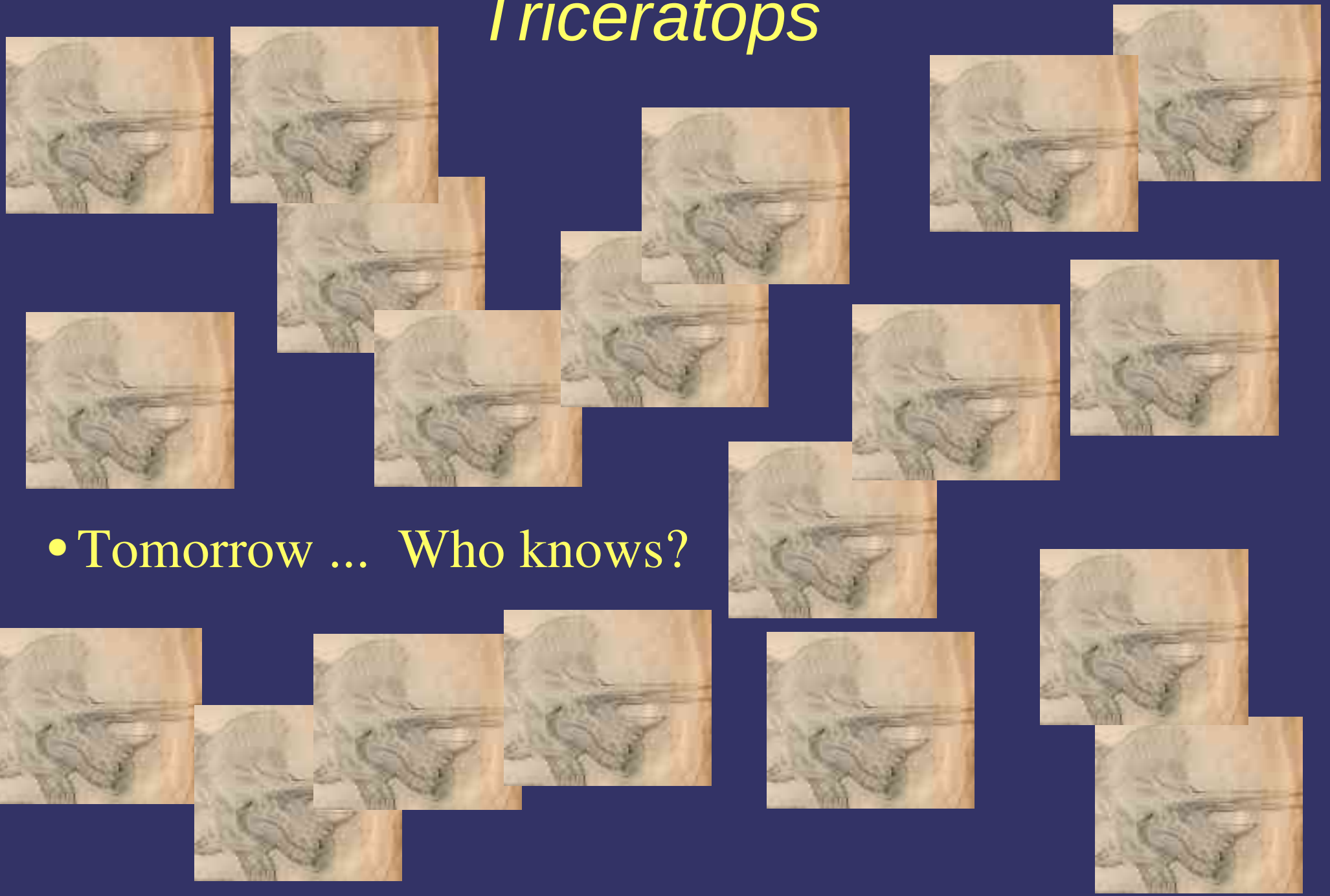
Dinosaur species – a case study: *Triceratops*

- No, wait! – only *one* species (Ostrom and Wellnhofer 1986; Lehman 1990)

Dinosaur species – a case study: *Triceratops*

- Today, there are two species (Forster 1990, 1996)

Dinosaur species – a case study: *Triceratops*



- Tomorrow ... Who knows?

Dinosaur species across the data-set

- Total number of species is 562 in 451 genera, for an average of 1.25 species per genera.
- 381 genera (85%) are monospecific.
- 46 genera have two species, 17 genera have three.
- Only seven genera have more than three species:
  - *Camarasaurus*, *Cetiosaurus*, *Chasmosaurus*, *Edmontonia* (4 species)
  - *Iguanodon*, *Mamenchisaurus* (7 species)
  - *Psittacosaurus* (8 species)
- ... And some of these are now squashed (*Cetiosaurus*).

Five reasons for varying apparent diversity

1. Geological preservational bias
2. Anatomical preservational bias
3. Differential splitting/lumping
4. Focus of current work
5. SPECIAL MYSTERY GUEST REASON

1. Geological preservational bias

- Raup (1972) observed a strong correlation between apparent diversity levels of marine invertebrates throughout the Phanerozoic era and the volume of available sediment.

(This observation does not make a nice, neat bullet point)

- Availability of sediment may be the single most significant factor affecting apparent diversity.

2. Anatomical preservational bias

- Theropods typically have light, hollow bones
- Sauropodomorphs and ornithischians usually have heavy, solid bones (except sauropod vertebrae)

  => Theropods should be preserved *less* often than other dinosaurs

- But we observe *more* theropod genera than sauropodomorphs or ornithischians

  => There must be other factors that outweigh this one.

3. Differential splitting/lumping

- "Glamorous" clades tend to be split more than others:
  - Everyone wants to name a new giant Morrison sauropod.
  - Everyone wants to name a new Tyrannosaur.
  - No-one wants to name a new basal ornithopod.
- Examples of over-split big sauropods:
  - "Ultrasauros" (Jensen 1985) is a *Supersaurus* vertebra and a *Brachiosaurus* scapula (Curtice et al. 1996)
  - "Seismosaurus" may be *Diplodocus* (Lucas in prep.)
  - Subgenus "Giraffatitan" (Paul 1988) is not different from *Brachiosaurus*.

4. Focus of current work

- Many more papers are published on theropods than on sauropods or ornithischians.
- This year's JVP abstracts include fourteen on tyrannosaurs alone – this may be more than for all ornithischians combined.
- Ornithopod specimens collected on expeditions remain in their jackets while the theropods are prepared, studied, described, publicised and recruited to star in *Jurassic Park XIV: Wrath of the Raptors*.
- "100 years of *Tyrannosaurus*" symposium coming up next year! (email from Ken Carpenter)

And now …

the
SPECIAL MYSTERY
GUEST REASON
for variation in apparent
diversity
…

5. Actual diversity

- The diversity of the real ancient ecosystem is the starting point for our observations.
- But actual diversity is so muddied by preservational and other biases that we need to be VERY CAREFUL in interpreting apparent diversity figures.
- The results of this study probably tell us more about dinosaur science than about the dinosaurs themselves.

Conclusions

- Theropods seem to be more diverse than either sauropodomorphs or ornithischians.
- Dinosaur diversity was high in the Carnian, and highest in the Kimmeridgian and late Cretaceous.
- The USA, China and Mongolia account for more than half of dinosaur genera between them.
- The rate of naming new dinosaur genera is increasing exponentially.
- Diversity figures can't be taken at face value because so many biases affect the apparent diversity.

Acknowledgements

- The database analysed in this study is based on that assembled by T. Mike Keesey for his Dinosauricon web-site.
- David M. Martill commented extensively on a draft of the manuscript on which this presentation is based.
- I would never even have started this work without Mathew J. Wedel's encouragement; and it would have been much less useful without his criticism. He should make his mind up.

The End

Source of data: `dinosauricon.com`

- A single data-set was used for all the analyses in this work.
- Taken with permission as XML from the web-site `http://dinosauricon.com/`
- Edited to remove data formatting errors.
- Updated with new genera to the end of 2001.
- Updated with information discovered since data was published, e.g. better dating of some type specimens.
- NOT edited to conform to my view of reality – e.g. *Giraffatitan* survives as a distinct genus.

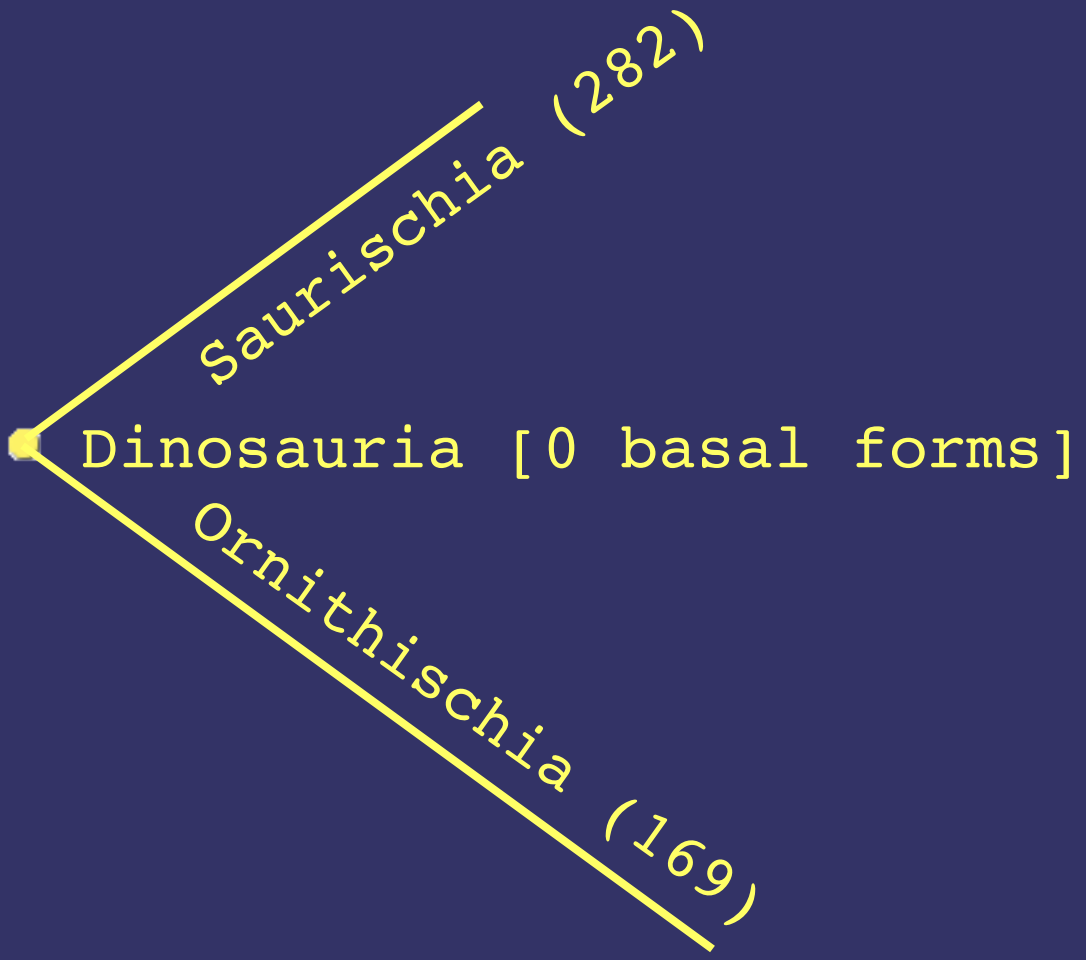
Why dinosauricon.com?

- IT'S THERE. Which is more than can be said for most other data-sets.
- There is NO equivalent peer-reviewed data-set.
- The Dinosauricon web-site is “published” in the broad sense of being generally available, and so is there to be criticised and corrected.
- In practice, it is probably the most reviewed dinosaur genus data-set in the world.
- Other workers have not been willing to share their databases.

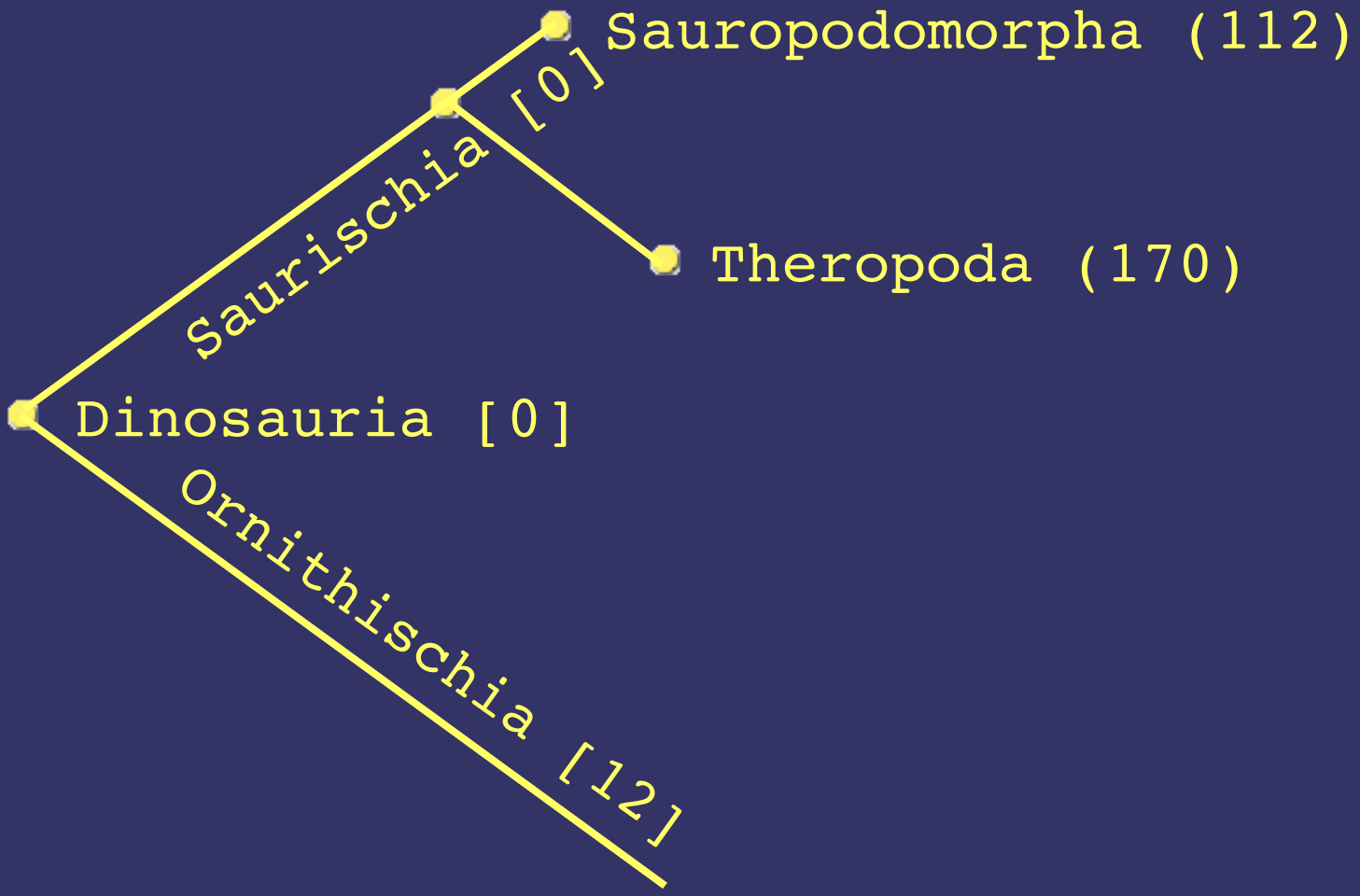
Results 1: number of genera by clade

- Dinosauria (451 genera)

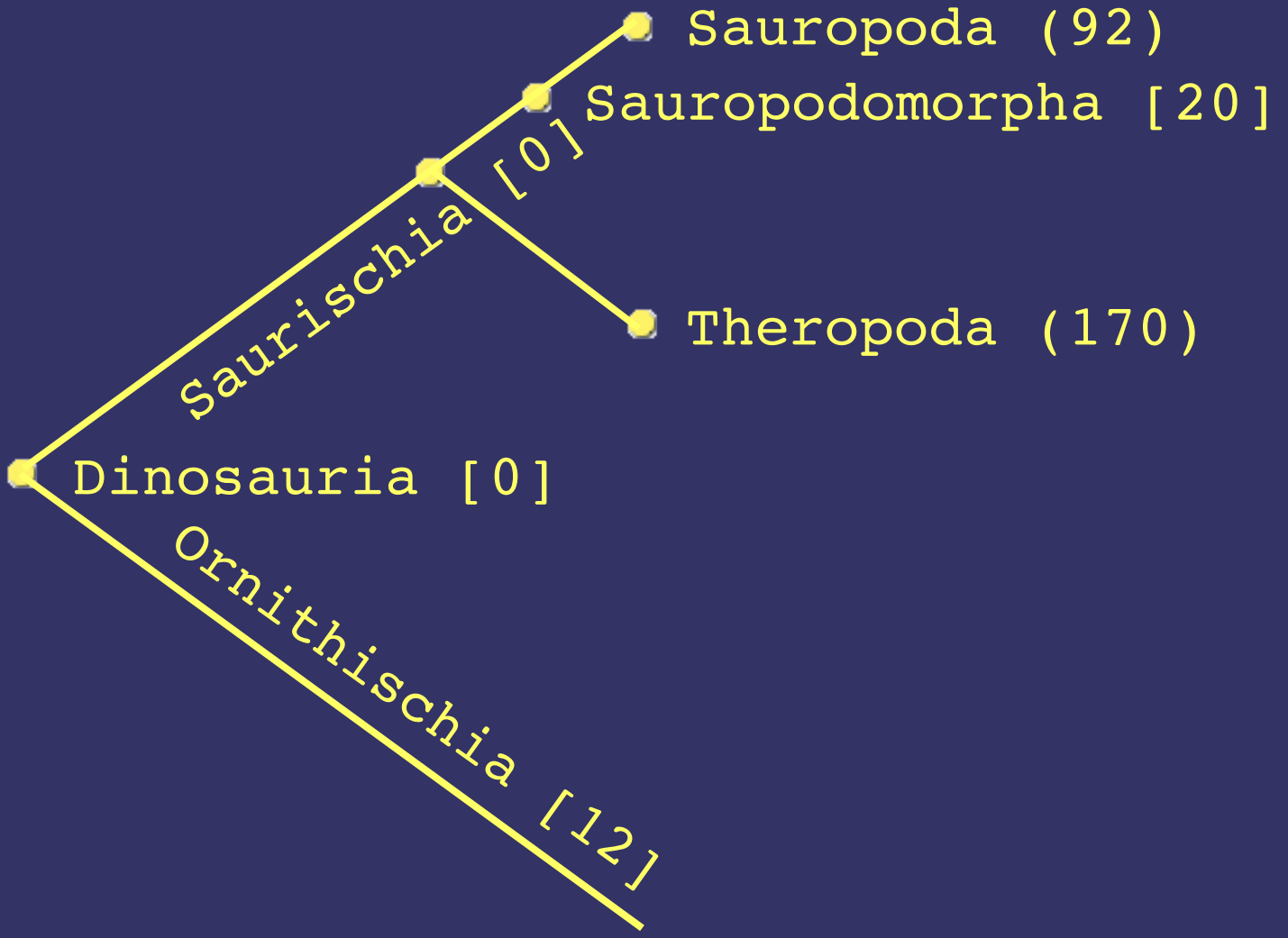
Results 1: number of genera by clade



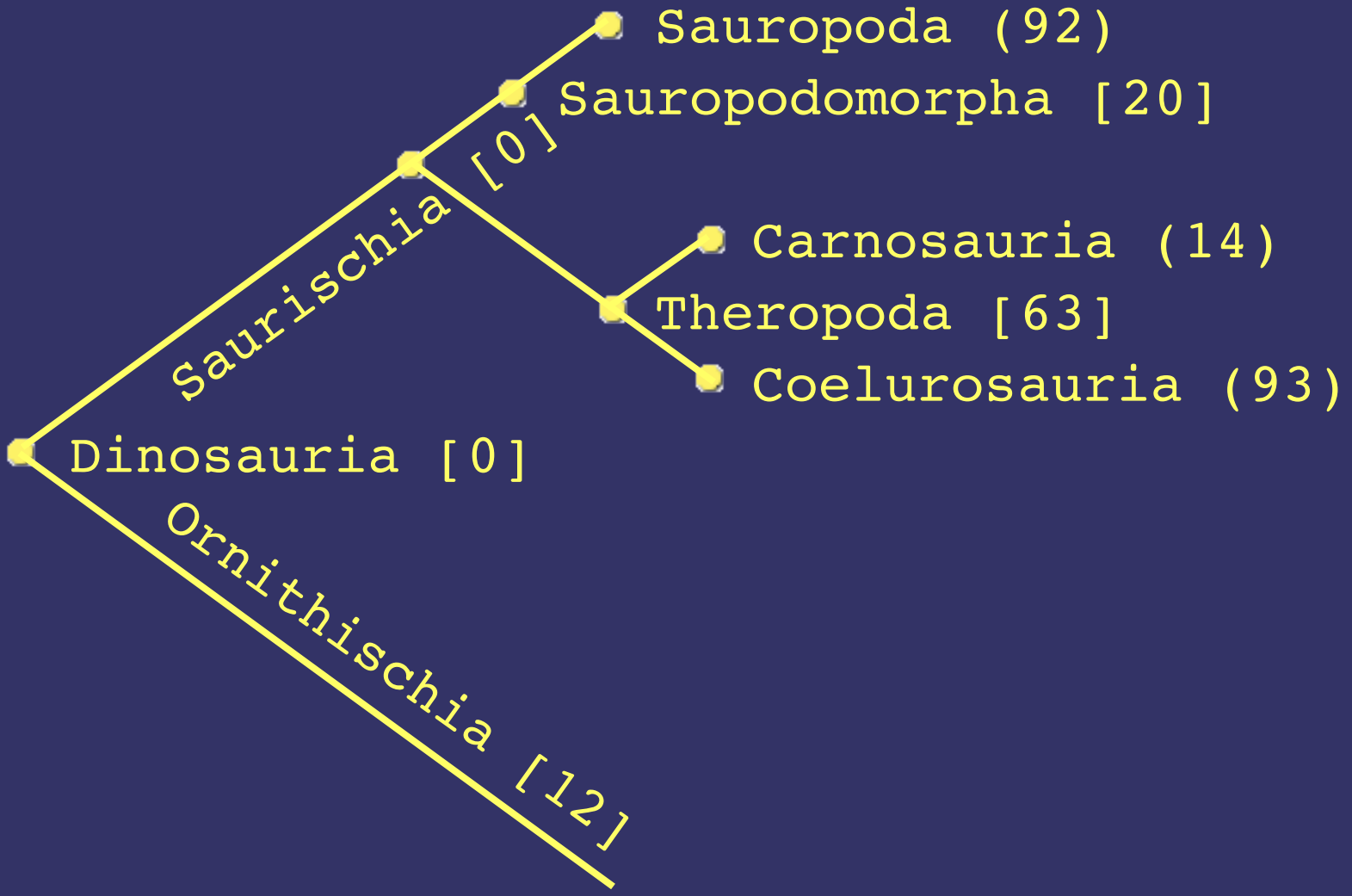
Results 1: number of genera by clade



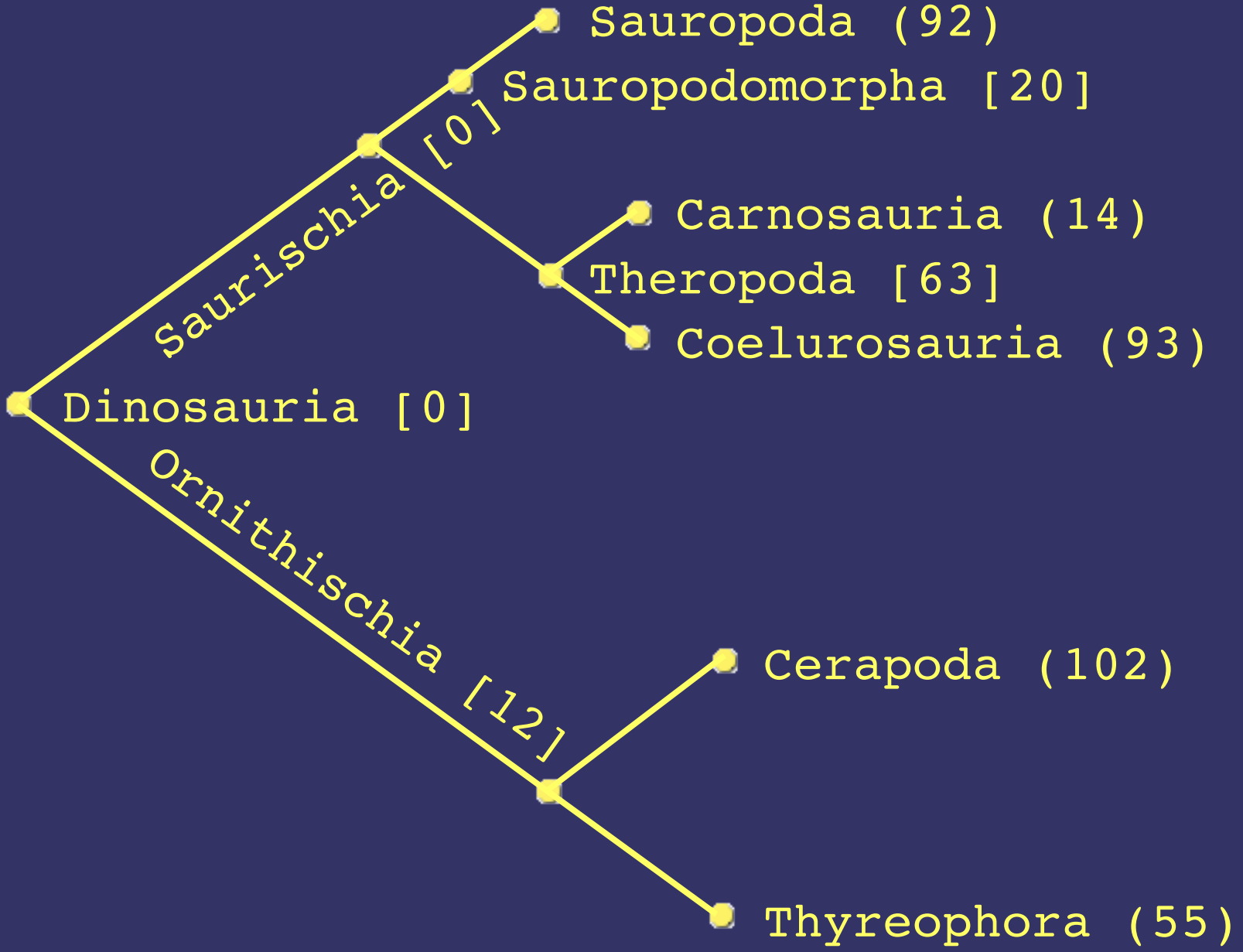
Results 1: number of genera by clade



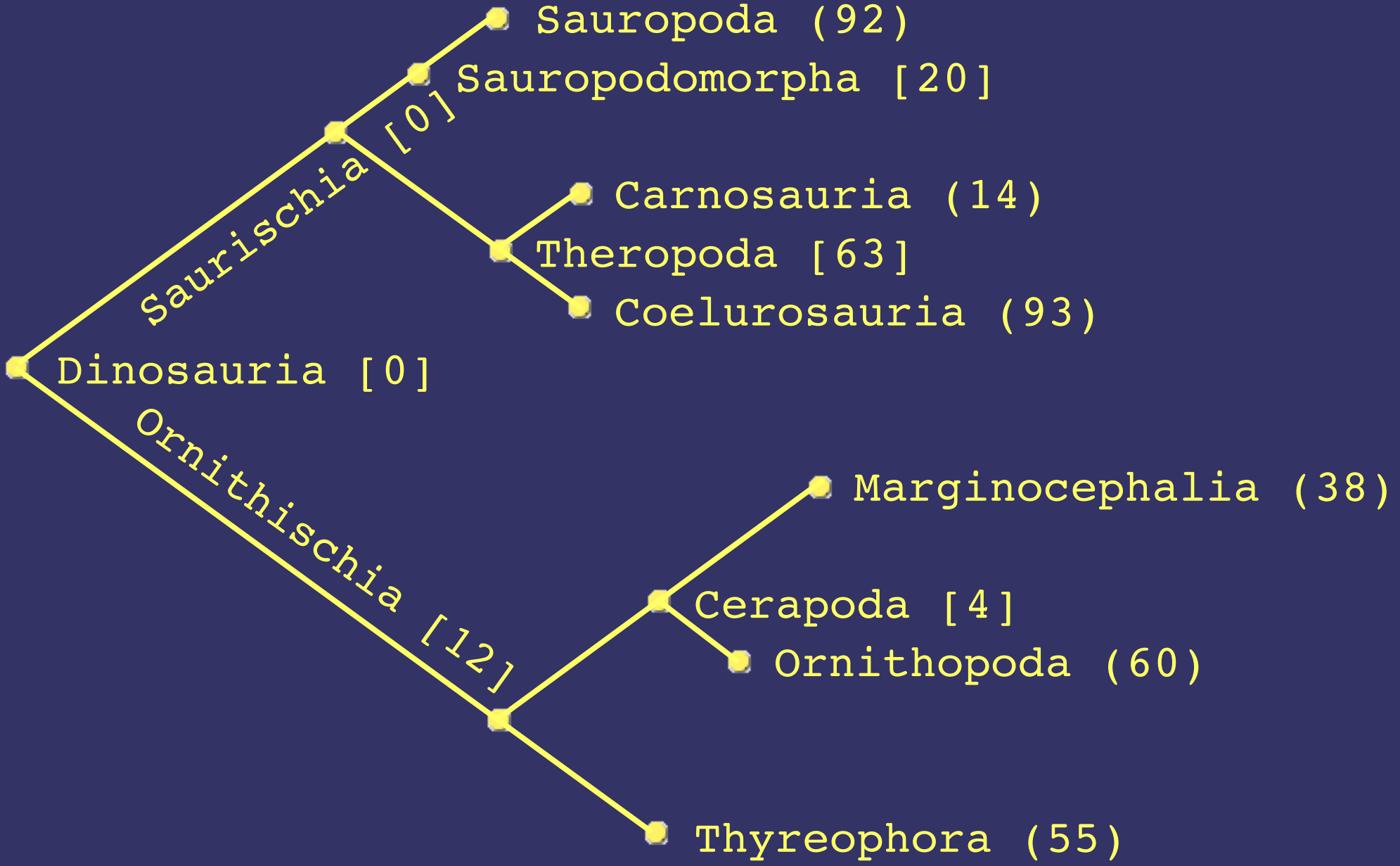
Results 1: number of genera by clade



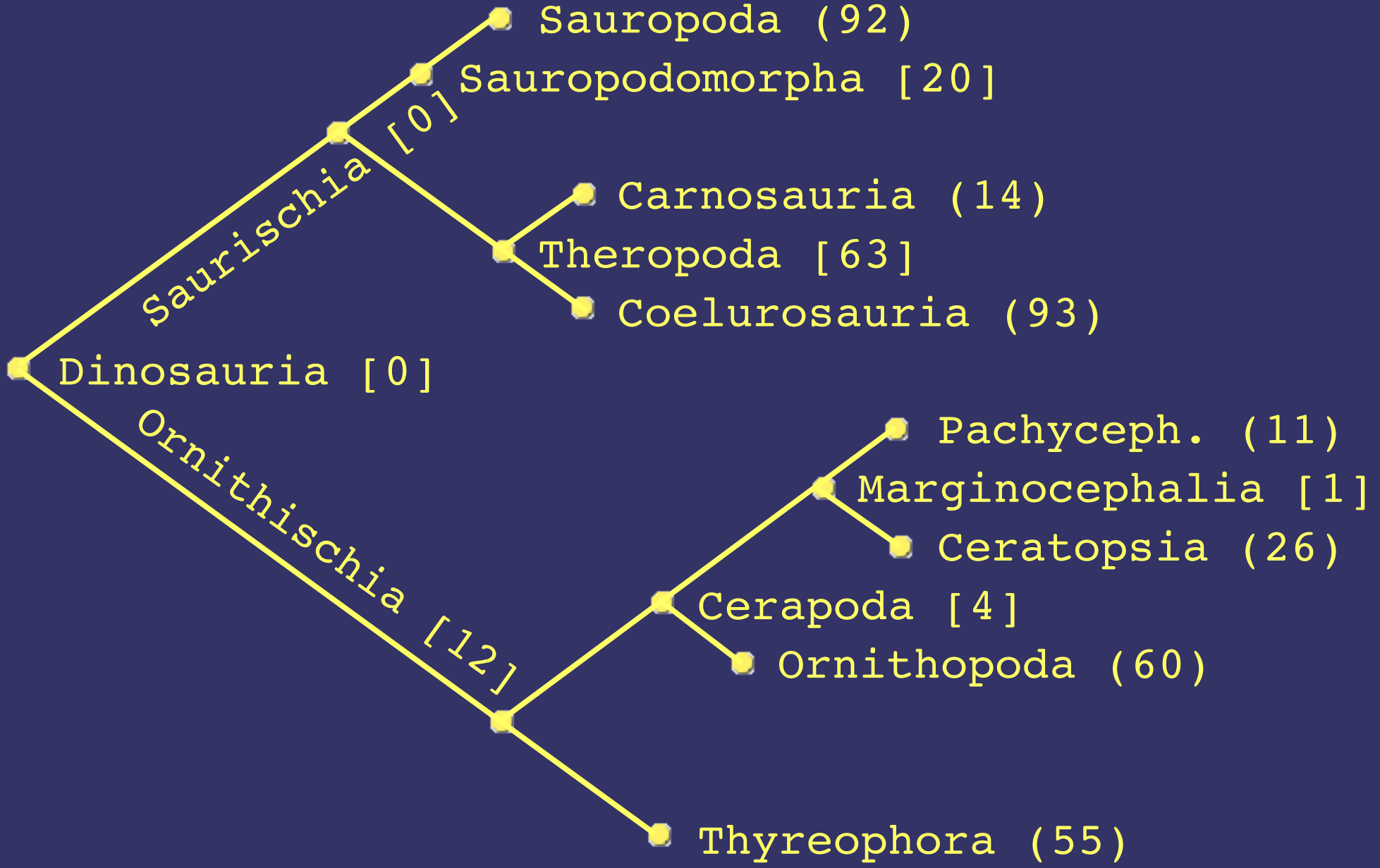
Results 1: number of genera by clade



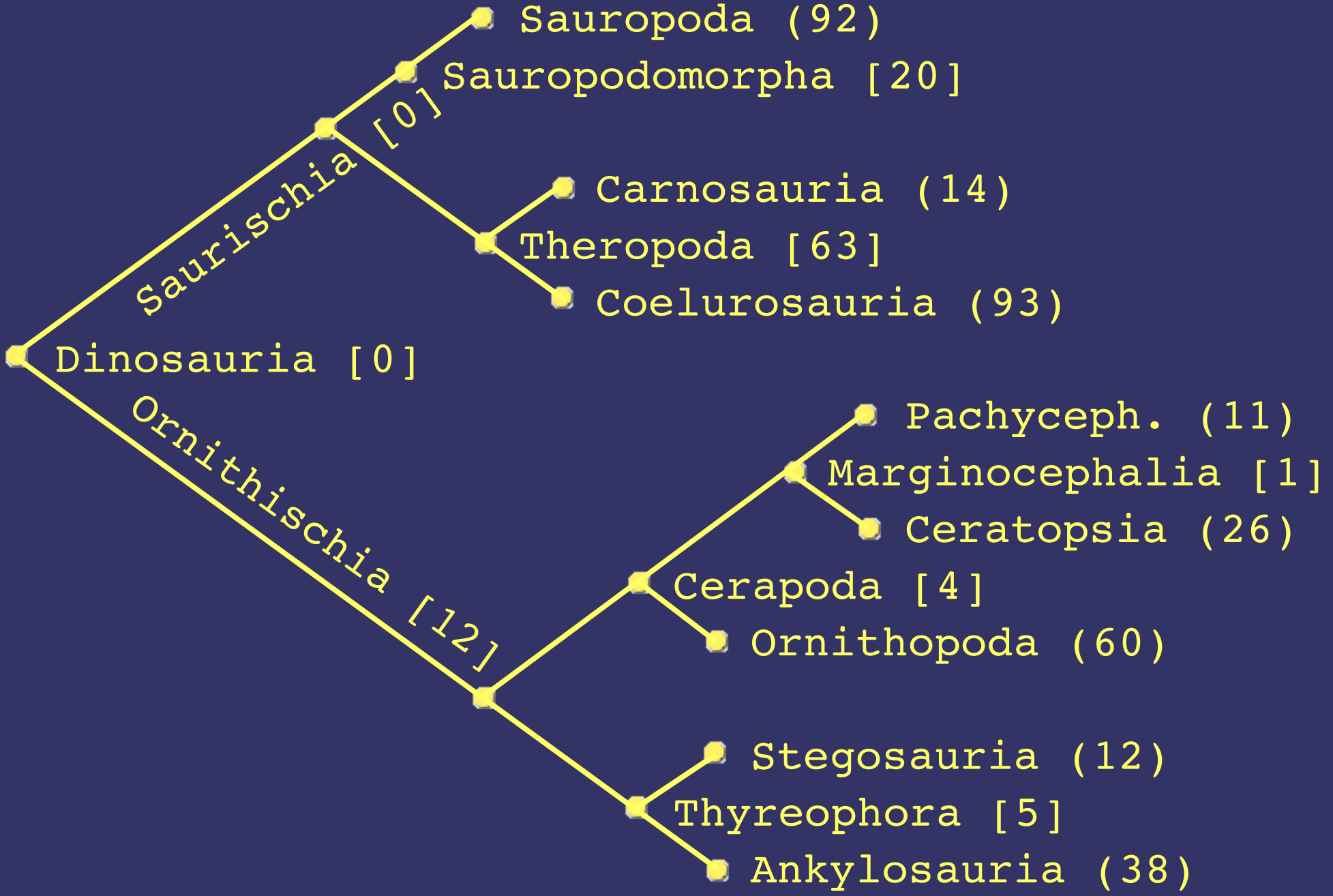
Results 1: number of genera by clade



Results 1: number of genera by clade



Results 1: number of genera by clade



Earliest occurrence of some clades

- Sauropoda – *Isanosaurus* – Norian
- Neosauropoda – *Atlasaurus* – Bathonian
- Diplodocoidea – [eleven genera] – Kimmeridgian
- Titanosauria – *Tendaguria* – Kimmeridgian
- Canosauria – *Cryolophosaurus* – Pliensbachian
- Coelurosauria – *Eshanosaurus* – Hettanginian
- Pachycephalosauria – *Yaverlandia* – Barremian
- Ceratopsia – *Chaoyangosaurus* – Middle Jurassic
- Ornithopoda – *Yandusaurus* – Bathonian
- Stegosauria – *Huatangosaurus* – Bathonian
- Ankylosauria – *Tianchisaurus* – Bathonian

Questionable early occurrences

- *Eshanosaurus* (Hettanginian) was described as a therizinosaur (Xu, Zhao and Clark 2001), but may be a prosauropod.
- *Yaverlandia* (Barremian) was described as a pachycephalosaur (Galton 1971) but has since been proposed as everything except a pebble.
- *Chaoyangsaurus* (Midddle Jurassic) is a good ceratopsian but predates *Archaeoceratops* by about forty million years.

The Kimmeridgian Sauropod Boom

- Twenty new sauropod genera in a single age!
- Morrison Formation

Amphicoelias
Apatosaurus
Barosaurus
Brachiosaurus
Camarasaurus
Diplodocus
Dyslocosaurus
Dystylosaurus
Eobrontosaurus
Haplocanthosaurus
Seismosaurus
Supersaurus

- Tendaguru

Dicraeosaurus
Giraffatitan
Janenschia
Tendaguria

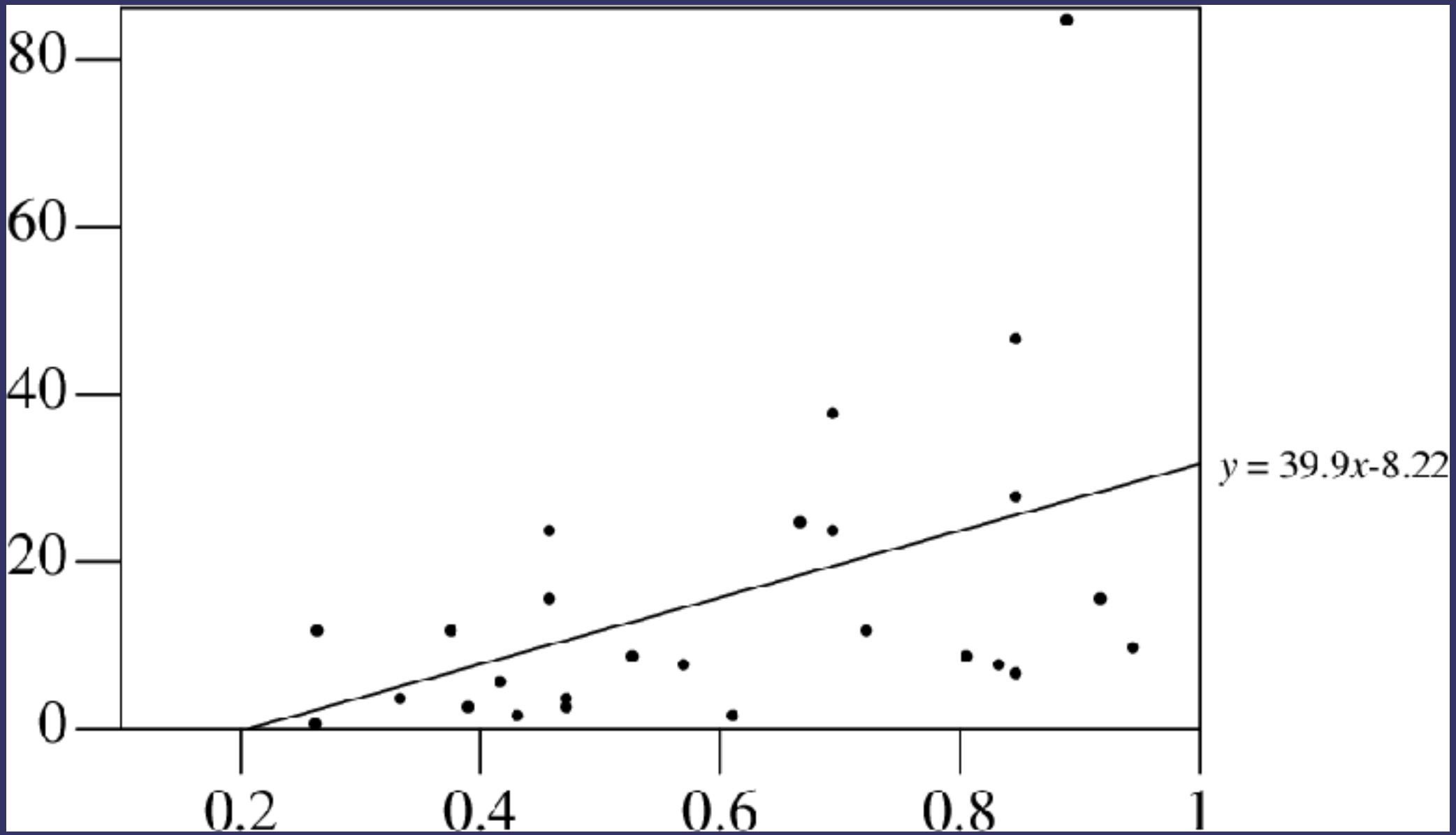
- China

Euhelopus
Omeisaurus

- Portugal

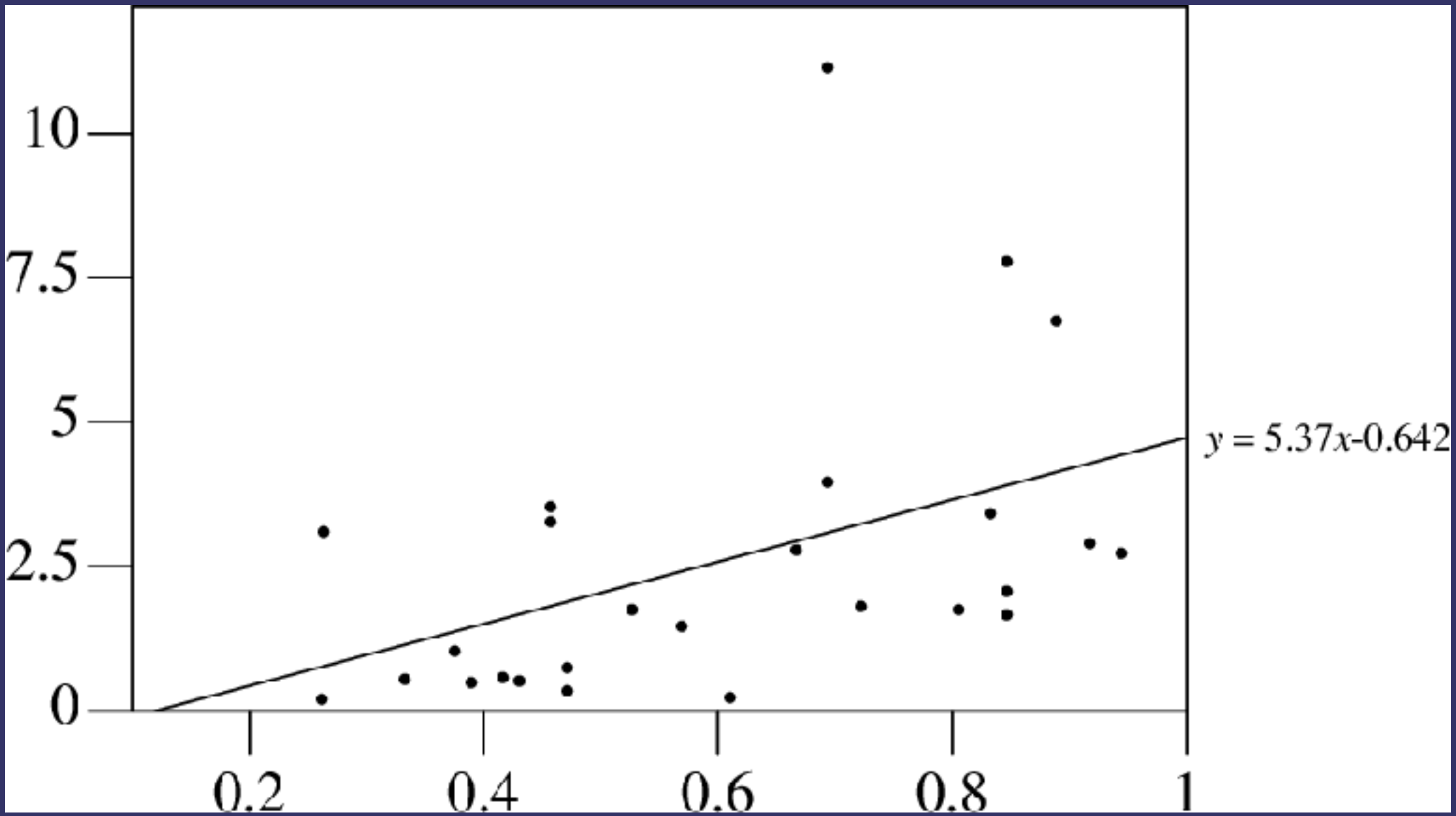
Dinheirosaurus
Lourinhasaurus

Number of genera (y) vs. coastal onlap (x)



Correlation coefficient = 0.471

Genus density (y) vs. coastal onlap (x)

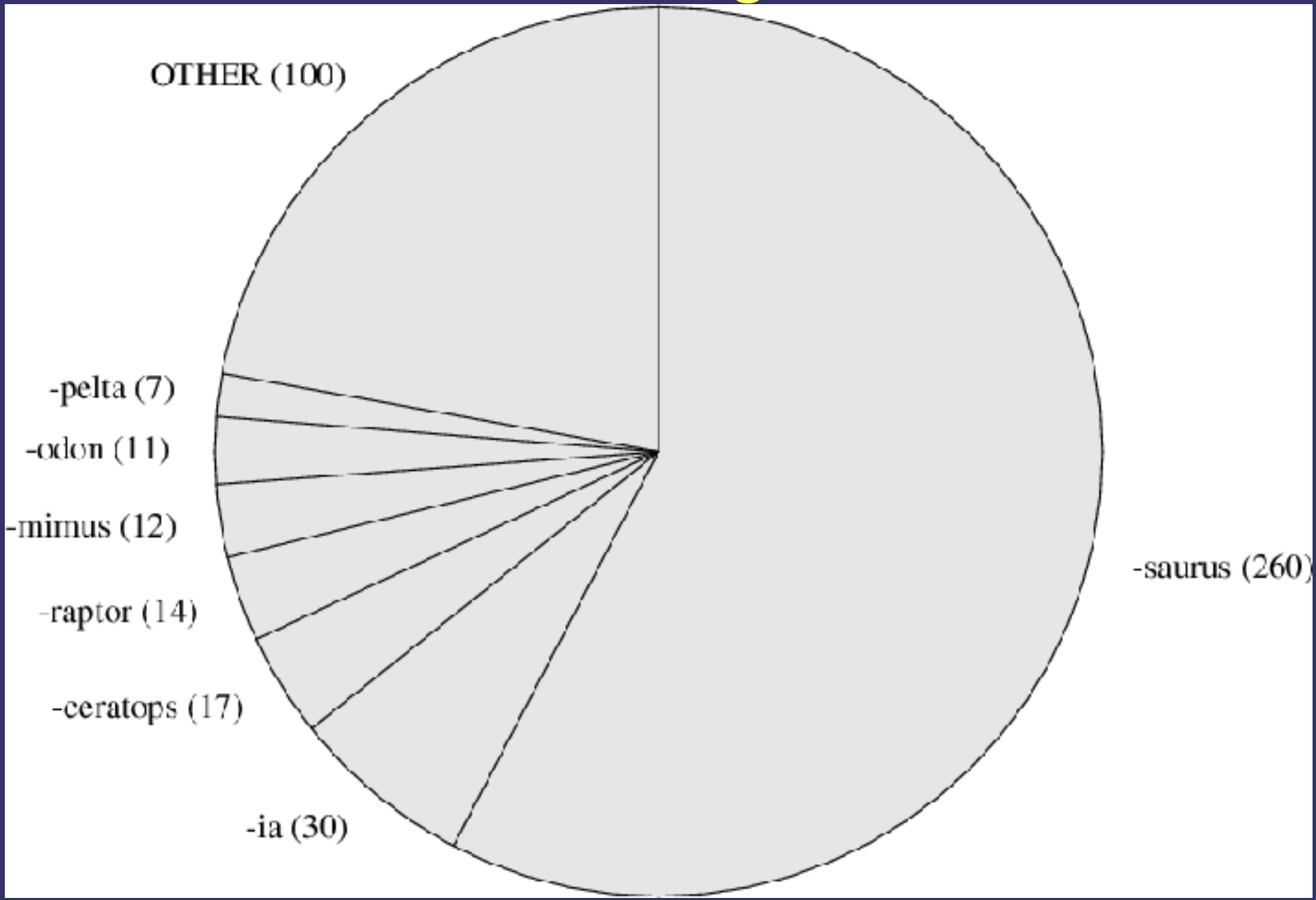


Correlation coefficient = 0.449

First dinosaur from each continent

- Europe – 1825 – *Iguanodon*
- Africa – 1854 – *Massospondylus*
- North America – 1856 – *Troodon*
- Asia – 1877 – *Titanosaurus*
- South America – 1893 – *Argyrosaurus*
- Australasia – 1925 – *Rhoetosaurus*
- Antarctica – 1994 – *Cryolophosaurus*
  - ... which completes the set

Results 5: dinosaur genera by name ending



Albertosaurus Amargasaurus
Aegyptosaurus Andesaurus Beipiaosaurus
Argentinosaurus
Cedarosaurus
Edmontosaurus
Atlasaurus Gobisaurus Jeholosauru

Enough with the *place*-saurus already!

Liaoningosaurus
Patagosaurus
Magyarosaurus
Malawisaurus Shantungosauru
Mavisenderbysaurus
Siamosaurus
Nemegtosaurus
Nipponosaurus
Nigersaurus Lesothosaurus
Laplatasaurus

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Lesothosaurus
Laplatasaurus

(Sorry, just had to get that off my chest.)

3. Ecological preservational bias

- Many theropods would have been opportunistic scavengers as well as hunters.
- They would favour environments, such as sea margins and lagoon shores, where carrion is abundant. These environments are conducive to fossilisation.
- Many herbivores would favour dryer plains, offering less likelihood of fossilisation.
- In some formations, theropods are the *only* known dinosaurs:
  - Solnhofen (three theropods)
  - Santana (four theropods)

A war-cry: dinosaur genus databases

- *The Dinosauria 2* will include a list of genera with dates, ages and countries of origin.
- Glut's *Dinosaurs: The Encyclopedia* and supplements consitute a similar database.
- Peter Dodson maintains his own database.
- At least two other workers I've spoken to have their own databases. There must be more.
- Now I have one, too.

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- NONE OF THESE DATABASES IS PEER REVIEWED.

Grand unified dinosaur genus database

- My day-job is to do with standards and sharing of information, so the many-databases situtation hurts.
- Much effort is wasted in maintaining similar databases.
- Each database is constantly going out of date.
- No-one has time to peer-review someone else's DB.

What's the answer?

- The solution is a single database maintained by expert consensus, and publicly available for anyone to use.
- At present, `dinosauricon.com` is the closest thing to this, which is why I based by own database on it.