

Temporal coverage of ammonoid measurement data in the Paleobiology Database

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Short Report

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Abstract

Large compilations of ammonoid shell measurements underpin studies of body-size evolution, conch-shape disparity and extinction selectivity, but how evenly those measurements sample the ammonoid record has not been tested. I compared 20,272 measured ammonoid specimens in the Paleobiology Database (PBDB) with 64,733 species-level PBDB occurrences spanning the Devonian to the Cretaceous. Measured specimens are over-represented relative to occurrences in the Carboniferous and Permian (about twice their occurrence share) and under-represented in the Jurassic and Cretaceous; the Cretaceous holds 30.8% of occurrences but 16.5% of dated measured specimens. The share of species with at least one measured specimen falls from 75.7% in the Permian to 27.5% in the Cretaceous. When 2,500 occurrences are drawn from each period 500 times, the gradient persists (Permian 78.4%, Cretaceous 32.1%) with non-overlapping 95% intervals. Leaving out each of 714 specimen references in turn never changes the sign of the Cretaceous deficit, but the Triassic excess and Carboniferous coverage depend heavily on a few large monographs. Heteromorph ammonoids are almost unmeasured (2.7% of 714 Cretaceous heteromorph species), yet excluding them raises Cretaceous coverage only to 34.7%. In a logistic model controlling for occurrence frequency, Cretaceous species have 7.6 times lower odds of being measured than Permian species. Analyses of ammonoid size or shape through time that draw on PBDB measurements therefore compare a densely measured Paleozoic and Triassic with a thinly measured Jurassic and Cretaceous, and should account for this imbalance.

1. Introduction

Ammonoids are among the best-studied groups for testing how size and shape evolve over long time spans. Their abundant, well-dated record and simple shell geometry have supported work on morphospace occupation (Saunders et al. 2004; Ritterbush and Bottjer 2012), disparity through extinction and recovery (Korn and Klug 2012; Whalen et al. 2020), and long-term body-size trends (Heim et al. 2015; Klug et al. 2025). These studies all rest on compilations of shell measurements, usually conch diameter, whorl height, whorl width and umbilical width (Korn 2010; Klug et al. 2015).

The fossil record is known to be unevenly sampled through time, and occurrence-based diversity studies routinely correct for this (Raup 1972; Alroy et al. 2001; Smith and McGowan 2007). Trait data face a second filter that is less often examined: of the species known from occurrences, only some have been measured and the measurements compiled. If that fraction varies through time, comparisons of size or shape between intervals may partly reflect uneven measurement effort rather than biology. Completeness metrics address a related problem for vertebrate skeletons (Mannion and Upchurch 2010), but I am not aware of an equivalent assessment for invertebrate morphometric compilations.

The Paleobiology Database (PBDB) offers a direct way to test this, because it holds both measured specimens and occurrences for the same taxa, linked through shared identifiers. Here I use a curated extract of both records (Chakraborty 2026) to ask three questions. First, is the PBDB ammonoid measurement record distributed through time in proportion to the occurrence record? Second, does any imbalance survive equal sampling and the removal of individual source publications? Third, how much of the imbalance is explained by heteromorphs, whose uncoiled shells do not suit standard conch measurements?

2. Materials and methods

2.1 Data

All analyses use the curated dataset of Chakraborty (2026), which was extracted from two PBDB downloads made on 24–25 September 2026 with the base taxon "ammonite", species-level resolution and all taxonomic statuses. The specimen table holds 20,272 measured specimen records of 5,316 accepted species from 762 references and 4,835 collections. The occurrence table holds 64,733 species-level occurrences of 11,547 accepted species from 2,524 references and 25,740 collections. Every dated specimen links to an occurrence in the occurrence table through its occurrence number. The dataset records which specimens were measured, not the measurement values, so no size or shape values are analysed here.

Of the specimen records, 4,121 are type specimens (2,733 holotypes and 1,388 paratypes). Where the source of a measurement is recorded, 14,390 came from tables, 2,640 from figures and 1,306 from text. 130 specimen records lack a collection and therefore an age; they are excluded from time-based analyses but retained when deciding whether a species has been measured.

2.2 Time assignment

Each record was assigned the midpoint of its PBDB age range and placed in the period containing that midpoint (Devonian 420–358.9 Ma, Carboniferous 358.9–298.9 Ma, Permian 298.9–251.9 Ma, Triassic 251.9–201.4 Ma, Jurassic 201.4–145 Ma, Cretaceous 145–66 Ma). Median age uncertainty is 3.8 Myr for dated specimens and 4.45 Myr for occurrences. For finer resolution, each record's age range was also divided among 5-Myr bins in proportion to its overlap with each bin, so that poorly dated records spread across several bins rather than falling into one. Species were assigned the most frequent period among their occurrences.

2.3 Representation and coverage

Two measures describe how well measurements track the record. Representation compares a bin's share of measured specimens with its share of occurrences, as $\log_2(\text{specimen share} \div \text{occurrence share})$; a value of + 1 means a bin holds twice as many measured specimens as its occurrences predict, and – 1 half as many. Species coverage is the percentage of species known from occurrences that have at least one measured specimen.

2.4 Sampling standardisation

Raw coverage falls as sampling increases, because heavily sampled intervals yield more rare, unmeasured species. To remove this effect, I drew a fixed number of occurrences (2,500, and 1,000 as a check) without replacement from each period, recorded the percentage of species in the draw that have been measured, and repeated this 500 times. This follows the logic of classical rarefaction used in diversity studies (Alroy et al. 2001). The smallest period sample is the Devonian, with 2,899 occurrences.

2.5 Sensitivity to individual references

To test whether a few publications drive the pattern, I removed the specimens of each of the 714 references that contribute dated specimens, one at a time, and recalculated representation and coverage for every period. I also removed the ten references with the most specimens together, which account for 23.4% of all specimen records.

2.6 Heteromorphs and a species-level model

Heteromorphs, ammonoids with partly or fully uncoiled shells, were identified at family level using 24 families listed in the dataset (for example Baculitidae, Scaphitidae, Turritidae, Ancyloceratidae and the Triassic Choristoceratidae). To separate the effect of shell form from the effect of time, I fitted a logistic regression predicting whether a species has been measured from its period (with the Permian as reference), a heteromorph indicator and the natural log of its number of occurrences, which controls for the fact that common species are more likely to be measured. The model covers all 11,547 species.

Analyses were run in Python with pandas and statsmodels, with a fixed random seed for the subsampling.

3. Results

3.1 Measurements are concentrated in the Paleozoic and Triassic

Measured specimens track the broad shape of the occurrence record (Spearman's $\rho = 0.69$ across 5-Myr bins) but are not proportional to it. Both records peak in the Early Triassic, with the 250–245 Ma bin holding the most measured specimens and the most occurrences. That peak is exaggerated in the measurements: records with midpoints between 252 and 247 Ma make up 17.7% of dated specimens but 10.1% of occurrences.

From the Carboniferous through the Triassic most bins are over-represented, while 21 of the 22 bins younger than 175 Ma are under-represented (Fig. 1). The earliest Devonian bins are also under-represented, but they contain few records. At period level the Carboniferous and Permian hold about twice their expected share of measured specimens, and the Cretaceous about half (Table 1).

Table 1. Measured specimens, occurrences and species coverage by period. Shares use dated records only.

Period	Dated measured specimens	Occurrences	Specimen share (%)	Occurrence share (%)	log2 ratio	Species	Species measured (%)
Devonian	1,001	2,899	5.0	4.5	+0.15	583	56.9
Carboniferous	2,588	4,023	12.8	6.2	+1.05	869	73.3
Permian	2,486	4,239	12.3	6.5	+0.91	1,105	75.7
Triassic	6,419	15,386	31.9	23.8	+0.42	2,929	51.3
Jurassic	4,332	18,249	21.5	28.2	-0.39	2,859	38.6
Cretaceous	3,316	19,937	16.5	30.8	-0.90	3,202	27.5

3.2 Species coverage falls from the Permian to the Cretaceous

Overall, 5,294 of 11,547 species (45.8%) have at least one measured specimen. Coverage peaks in the Permian (75.7%) and falls through each Mesozoic period to 27.5% in the Cretaceous (Table 1). The same gradient appears across orders: Goniatitida are 73.5% covered and Prolecanitida 68.8%, but Ammonitida, the largest order with 5,823 species, only 32.3%. Common species are well covered, with 77.5% of the 200 most frequently occurring species measured, so the gap lies mainly among species with few occurrences.

3.3 The gradient survives equal sampling

Drawing 2,500 occurrences from every period leaves the ranking unchanged (Fig. 2). Cretaceous coverage is 32.1% (95% interval 30.7–33.7%) against 78.4% (77.1–79.6%) in the Permian, and no two periods have overlapping intervals. Draws of 1,000 occurrences give slightly higher values everywhere but the same order.

3.4 The Cretaceous deficit is robust; the Triassic excess is not

Removing any single reference never changes the sign of the representation value for the Carboniferous, Permian, Triassic, Jurassic or Cretaceous, and the Cretaceous has the lowest coverage in all 714 runs (Table 2). The Cretaceous is also the least sensitive period: no single reference shifts its representation by more than 0.10 or its coverage by more than 1.2 percentage points.

Removing the ten largest references together separates robust from fragile signals. The Cretaceous deficit shrinks but remains (−0.52), and the Permian excess grows (+1.30). The Triassic excess almost disappears (+0.09) and Triassic coverage drops from 51.3% to 36.5%. Carboniferous coverage drops from 73.3% to 45.2%.

Table 2. Sensitivity of representation (log2 ratio) and species coverage to source references. Ranges are across 714 runs, each omitting one reference. "Top 10 removed" omits the ten references with the most specimens together.

Period	log2 ratio (all data)	log2 range, one reference removed	Coverage (%), all data	Coverage range (%), one reference removed	log2 ratio, top 10 removed	Coverage (%), top 10 removed	Most influential reference
Devonian	+0.15	−0.21 to +0.24	56.9	43.9–56.9	+0.54	56.9	Bogoslovsky (1969)
Carboniferous	+1.05	+0.77 to +1.13	73.3	58.8–73.3	+0.74	45.2	Ruzhentsev and Bogoslovskaya (1971, 1978)
Permian	+0.91	+0.76 to +1.00	75.7	63.9–75.7	+1.30	75.7	Ruzhentsev (1956); Zhao et al. (1978)
Triassic	+0.42	+0.22 to +0.46	51.3	39.0–51.3	+0.09	36.5	Tozer (1994)
Jurassic	−0.39	−0.53 to −0.31	38.6	33.2–38.6	−0.49	30.8	Jeannet (1951)
Cretaceous	−0.90	−1.00 to −0.82	27.5	26.4–27.5	−0.52	27.5	Alsen (2006)

Table 3. Species coverage of coiled and heteromorph species by period.

Period	Coiled species	Coiled measured (%)	Heteromorph species	Heteromorph measured (%)
Devonian	583	56.9	0	—
Carboniferous	869	73.3	0	—
Permian	1,105	75.7	0	—
Triassic	2,911	51.5	18	11.1
Jurassic	2,844	38.8	15	6.7
Cretaceous	2,488	34.7	714	2.7

The ten largest references are Tozer (1994), Ruzhentsev and Bogoslovskaya (1971, 1978), Jeannet (1951), Hillebrandt (2006), Kummel and Steele (1962), Brayard and Bucher (2008), Gamsjäger (1982), Monnet and Bucher (2005) and Gabilly (1976). Five cover Triassic ammonoids, two Carboniferous and three Jurassic; none covers the Cretaceous.

3.5 Heteromorphs are nearly unmeasured but do not explain the gap

The dataset contains 747 heteromorph species, 714 of them Cretaceous, but only 51 measured heteromorph specimens. Just 2.7% of Cretaceous heteromorph species have a measurement, against 34.7% of coiled Cretaceous species (Table 3). Heteromorphs make up 22.3% of Cretaceous species and almost none elsewhere, so they depress Cretaceous coverage. Excluding them, however, raises Cretaceous coverage only from 27.5% to 34.7%, still less than half the Permian value.

The logistic model confirms that time and shell form act independently (Table 4). Each doubling of a species' occurrences raises its odds of being measured by a factor of about 1.43 (1.671 per unit of log occurrences). With occurrence frequency held constant, heteromorphs have about 22 times lower odds of being measured than coiled species. Cretaceous species have 7.6 times lower odds than Permian species even after heteromorphs are accounted for, and fitting the model to coiled species alone gives the same Cretaceous odds ratio (0.132).

Table 4. Logistic regression of whether a species has at least one measured specimen (n = 11,547 species; McFadden's pseudo-R² = 0.146). Reference period: Permian.

Predictor	Odds ratio	95% interval	p
ln (number of occurrences)	1.671	1.604–1.741	< 0.001
Heteromorph	0.046	0.030–0.072	< 0.001
Devonian	0.364	0.293–0.454	< 0.001
Carboniferous	0.779	0.633–0.959	0.018
Triassic	0.294	0.251–0.345	< 0.001
Jurassic	0.154	0.131–0.181	< 0.001
Cretaceous	0.132	0.112–0.156	< 0.001

4. Discussion

4.1 Why the measurement record is tilted toward the Paleozoic

Three factors plausibly combine. The first is the legacy of large taxonomic monographs that report dimensions in tables. Most measurements with a recorded source came from tables (14,390 of 18,336), and the references that most influence the Paleozoic and Triassic signals are such monographs (Table 2). When a single work describing hundreds of species with tabulated dimensions is entered into the database, it lifts the coverage of its interval in one step. The jackknife shows this directly: the Triassic excess and much of the Carboniferous coverage depend on a handful of works, while the Cretaceous deficit barely moves.

The second factor is the direction of morphometric research. Quantitative work on conch geometry has concentrated on Paleozoic and Early Triassic ammonoids, from Saunders et al. (2004) and Korn and Klug (2012) to Whalen et al. (2020), who measured 749 Paleozoic–Induan species. That tradition has produced standardised descriptive schemes (Korn 2010) that encourage authors to publish full dimension tables. Much of this effort sits outside PBDB, for example in the AMMON database (Korn and Ilg 2007), so the imbalance documented here describes PBDB, not the literature as a whole.

The third factor is shell form. Standard conch parameters assume a planispiral shell, and they do not describe straight, hooked or helical heteromorphs well. Heteromorphs are almost absent from the measurement record, and their concentration in the Cretaceous lowers that period's coverage. They are not the main cause, however: coiled Cretaceous species are also poorly measured, and the model gives the same Cretaceous odds ratio with or without them.

4.2 Consequences for size and shape studies

Any analysis that uses PBDB ammonoid measurements to compare intervals draws on samples of very different completeness. A Permian bin represents about three-quarters of its known species; a Cretaceous bin represents about a quarter to a third, excludes almost all heteromorphs, and is weighted toward common species. If measured species differ systematically from unmeasured ones in size or shape, for example because large, well-preserved or ornamented species are figured and measured more often, then between-period contrasts will carry that difference.

This does not mean that published results are wrong. Major syntheses have used other sources: Heim et al. (2015) took genus sizes from the *Treatise on Invertebrate Paleontology*, and Klug et al. (2025) compiled maximum sizes per stage from the literature and museum collections and analysed ammonoids without heteromorphs. Different compilations will have different gaps. The point is that coverage should be measured and reported alongside any trait-through-time analysis, because it is not uniform and cannot be assumed away.

Four practical steps follow. Report species coverage per time bin with any PBDB-based trait analysis. Test whether results hold when each bin is subsampled to equal coverage or when the largest source references are dropped. Treat heteromorphs separately, since they are effectively missing from the measurement record. Prioritise entering Cretaceous and Jurassic monographs with dimension tables, where each new reference adds the most information.

4.3 Limitations

Coverage is measured relative to the PBDB occurrence record, which is itself an uneven sample of past diversity (Smith and McGowan 2007). A species absent from PBDB occurrences cannot be counted as unmeasured, so true coverage is likely lower than reported here. Assigning records to periods by age midpoint misplaces some records whose ranges cross a boundary, although the 5-Myr analysis, which spreads records across bins, gives the same pattern. Heteromorphs are classified at family level, and a few families mix coiled and uncoiled forms. Finally, the dataset records whether a specimen was measured but not which dimensions, so a species with a single diameter counts the same as one with a full set of conch parameters. The analysis is a snapshot of a database that is continually updated; the access dates in Chakraborty (2026) define it.

5. Conclusions

1. PBDB ammonoid measurements are not proportional to the occurrence record. The Carboniferous and Permian hold about twice their expected share of measured specimens and the Cretaceous about half.
2. Species coverage falls from 75.7% in the Permian to 27.5% in the Cretaceous, and the gradient persists when every period is sampled equally.
3. The Cretaceous deficit is robust to removing any single reference, whereas the Triassic excess and Carboniferous coverage depend on a few large monographs.
4. Heteromorphs are almost entirely unmeasured, but excluding them closes only a small part of the Cretaceous gap.
5. Studies of ammonoid size or shape through time that use PBDB measurements should report and test for uneven coverage between time bins.

Declarations

Data availability

All data analysed here are openly available on Zenodo under a CC0 1.0 licence (Chakraborty 2026, <https://doi.org/10.5281/zenodo.22957954>). The source data are from the Paleobiology Database (<https://paleobiodb.org>).

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Competing interests

The author declares no competing interests.

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15. *Note on source monographs*. The references named in Table 2 and Section 3.4 (Bogoslovsky 1969; Ruzhentsev 1956; Ruzhentsev and Bogoslovskaya 1971, 1978; Zhao et al. 1978; Tozer 1994; Jeannet 1951; Hillebrandt 2006; Kummel and Steele 1962; Brayard and Bucher 2008; Gamsjäger 1982; Monnet and

Bucher 2005; Gabilly 1976; Alsen 2006) are PBDB source records identified by author and year in the dataset.

Figures

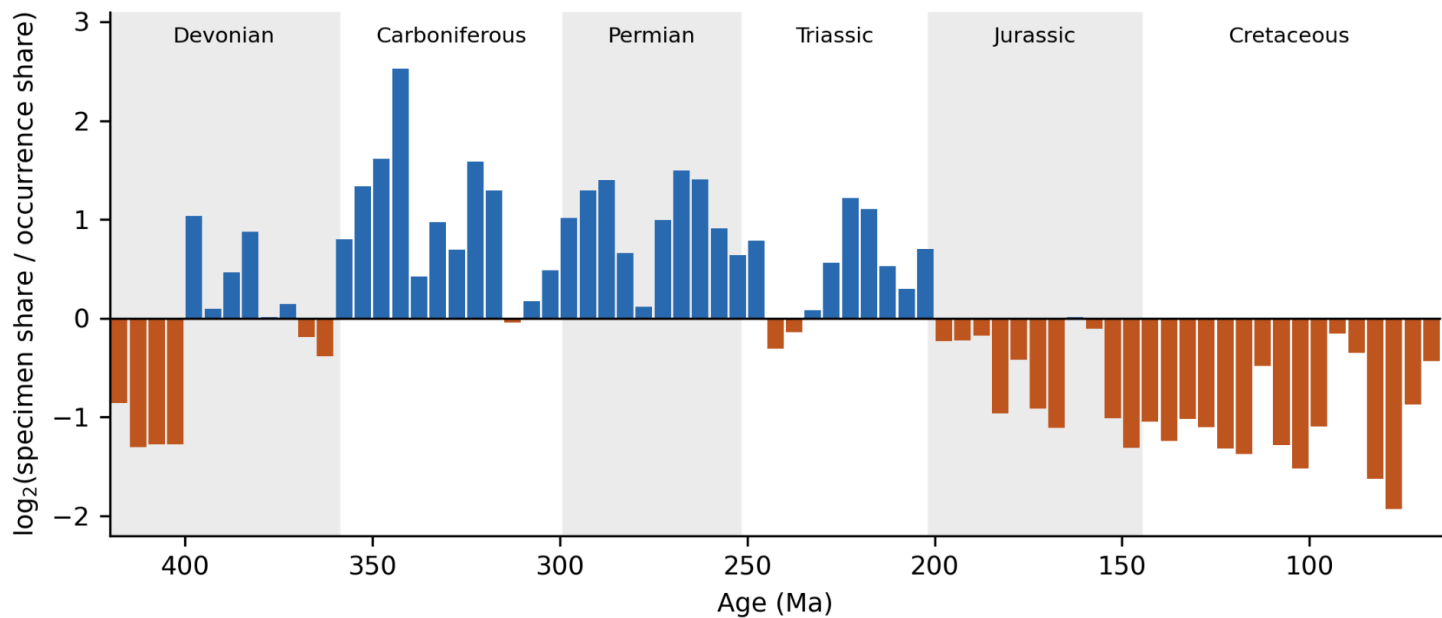


Figure 1

Representation of measured ammonoid specimens relative to PBDB occurrences in 5-Myr bins, 420–65 Ma. Each bar is $\log_2$ of a bin's share of dated measured specimens divided by its share of occurrences; +1 means twice the expected share and -1 half. Records are divided among bins in proportion to their age ranges. Shading marks periods. Data: Chakraborty (2026).

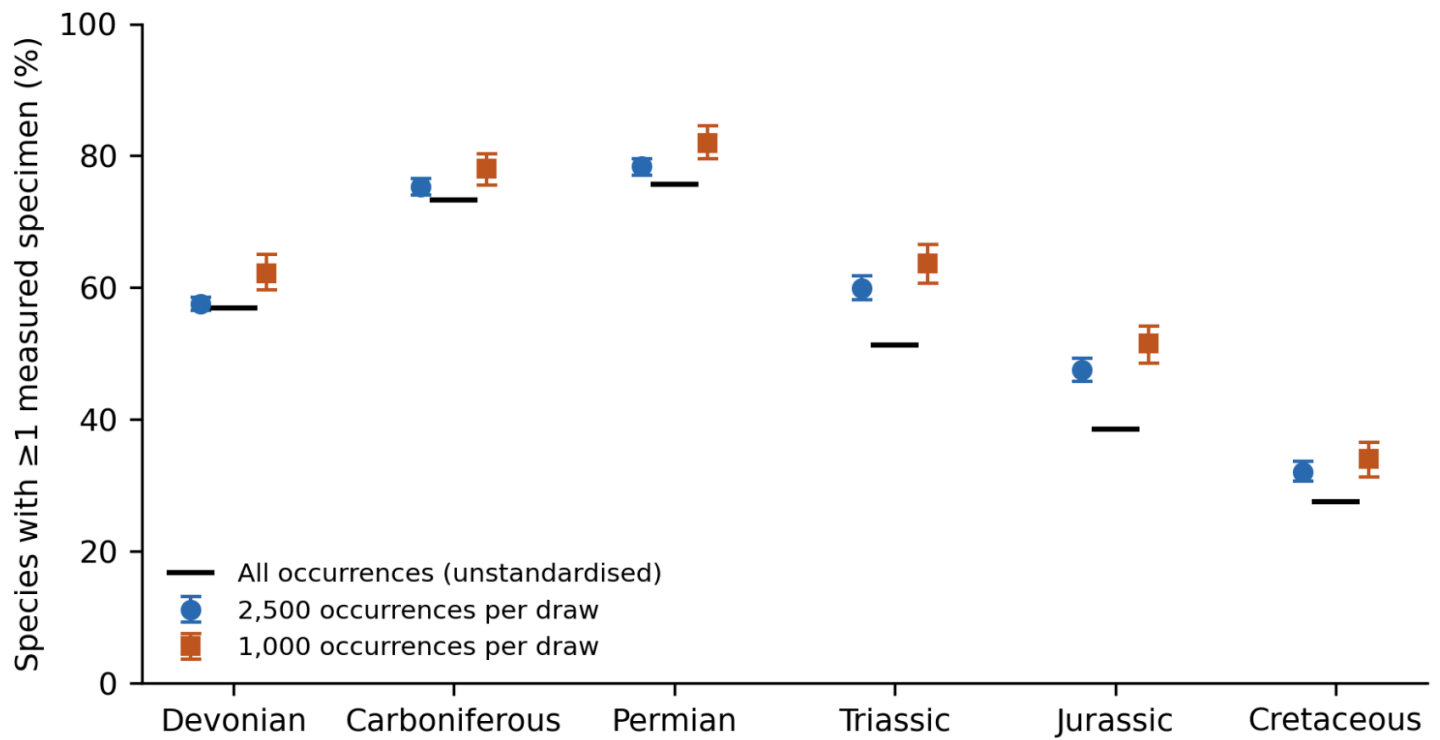


Figure 2

Percentage of ammonoid species with at least one measured specimen when an equal number of occurrences is drawn from each period (500 draws). Symbols are means and whiskers 95% intervals. Horizontal bars show unstandardised coverage (Table 1). Data: Chakraborty (2026).